PLANT PHYSIOLOGY & ECOLOGY

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TEXT-BOOK OF BOTANY

PLANT PHYSIOLOGY & ECOLOGY

(FOR DEGREE STUDENTS)

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Preface

This book is coming before you after quite a long gap of absence of any reliable text book for the students and teachers in Maharashtra. General books of Physiology, Ecology and Phytogeography were written separately by various authors which failed to satisfy the needs of the area. We have attempted to give a text book with uptodate knowledge at a very reasonable price which covers the syllabus of several universities including Nagpur University, Amrawati University, Aurangabad University and the universities of Madhya Pradesh also.

We are greatly obliged to many of our friends especially Dr. Pawar. Our sincere thanks are specially due to Shri B.B.S.P. Nag of Sindhu Mahavidyalaya who had given valuable suggestions from time to time.

We have pleasure in expressing our thanks to M/s. S. Chand & Company Ltd, specially to Mr. Bhagirath Kaushik, Manager of Nagpur branch who has taken very keen interest and given proper encouragement in bringing this book up to you.

As authors we will be very glad to receive the constructive suggestions from our teachers and students which may help us in its improvisation in future.

Despite the limitations due to price, we have attempted to give our best and hope that this venture will be welcomed.

AUTHORS

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1

Imbibition, Diffusion and Osmosis

The movement of materials into and out of the cells in plants takes place in solution or gaseous form. Although the exact process of this is not very clear, three physical processes are usually involved in it. They are **Imbibition**, **Diffusion** and **Osmosis**.

IMBIBITION

Certain substances if placed in a particular liquid absorb it and swell up. For example, when some pieces of gum or a piece of dry wood or dry seeds are placed in water they absorb the water quickly and swell up considerably so that their volume is increased. These substances are called as imbibants and the phenomenon as **imbibition**.

There exists certain force of attraction inbetween the imbitant and the imbibed substance. In plants this is because of the presence of a large number of **hydrophilic colloids** both in living as well as dead cells in the form of proteins, carbohydrates such as starch, cellulose, pectic substances etc. which have strong attraction towards water.

Imbibition plays a very important role in the life of the plants :—

- The first step in the absorption of water by the roots of higher plants is the imbibition of water by the cell walls of the root hairs.
- Imbibition of water is very essential for dry seeds before they start germination.

As a result of imbibition a pressure is developed which is called as **imbibition pressure**. The magnitude of this pressure is tremendous if the imbibant is confined (*i.e.*, closed) and allowed to imbibe so much so that a rock can be splited if some dry wooden

pieces are inserted in a small crack in that rock and then soaked with water.

DIFFUSION

If a small bottle filled with some gas or vapours is opened at a certain place in the room, very soon its molecules become evenly distributed throughout the available space in that room. Similarly, if a solute is placed in its solvent it is dissolved and its particles move so that they are evenly distributed throughout the container. This **movement of particles or molecules from a region of higher concentration to a region of lower concentration is called as diffusion**. The rate of diffusion of gases is faster than liquids or solutes.

The diffusing particles have a certain pressure called as the **diffusion pressure** which is directly proportional to the number or concentration of the diffusing particles. Therefore, the diffusion takes place always from a region of higher diffusion pressure to a region of lower diffusion pressure *i.e.*, along a **diffusion pressure gradient**.

The rate of diffusion increases if

(*i*) the diffusion pressure gradient is steeper

(*ii*) the temperature is increased

(*iii*) the density of the diffusing particles is lesser

(*iv*) the medium through which diffusion occurs is less concentrated.

Diffusion of more than one substances at the same time and place may be at different rates and in different directions but is independent of each other. A very common example of this is the gaseous exchange in plants.

Besides osmotic diffusion (see osmosis) the above-mentioned simple diffusion also plays a very important role in the life of the plants :—

- It is an essential step in the exchange of gases during respiration and photosynthesis.
- During passive salt uptake the ions are absorbed by simple process of diffusion.
- Last step in stomatal transpiration is the diffusion of water vapours from the intercellular spaces into the outer atmosphere through open stomata.

OSMOSIS

If a solution and its pure solvent are separated by a semi-permeable membrane (which allows only solvent and not the solute to pass through it) the solvent molecules diffuse into the solution. This diffusion of solvent molecules into the solution through a semi-

permeable membrane is called as **osmosis** (sometimes called as **osmotic diffusion**).

In case there are two solutions of different concentrations separated by the semi-permeable membrane, the diffusion of solvent will take place from the less concentrated solution into the more concentrated solution till both the solutions attain equal concentration.

The phenomenon of osmosis can be demonstrated by the following simple experiment : –

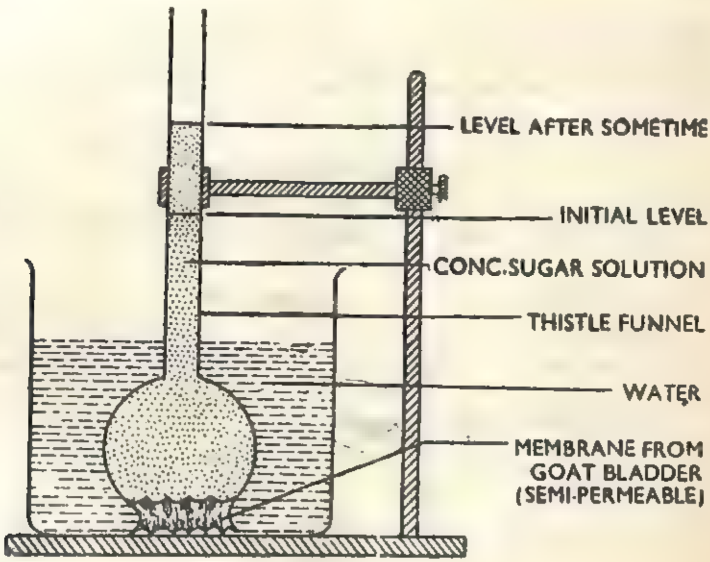


Fig. 1 . Demonstration of osmosis

Mouth of a thistle funnel is tied with goat bladder (it acts as semi-permeable membrane) and concentrated sugar solution is filled in it whose level is marked on its narrow neck. It is now placed in a beaker of water. After sometimes the level of the sugar solution in the thistle funnel rises (Fig. 1).

Osmotic Pressure. As a result of the separation of solution from its solvent or the two solutions by the semi-permeable membrane, a pressure is developed in solution due to the presence of dissolved solutes in it. This is called as **Osmotic Pressure** (**O.P.**)

- Osmotic pressure is measured in terms of atmospheres.

- Osmotic pressure is directly proportional to the concentration of dissolved solutes in the solution. More conc. solution has higher osmotic pressure.

- Osmotic pressure of solution is always higher than its pure solvent.

● Osmotic pressure does not increase by the addition of **insoluble solute** in the solution.

Thus, during osmosis the movement of solvent molecules takes place from the solution whose osmotic pressure is lower (*i.e.*, less concentrated or **hypotonic**) into the solution whose osmotic pressure is higher (*i.e.*, more concentrated or **hypertonic**).

Osmotic Diffusion of solvent molecules will not take place if the two solutions separated by the semi-permeable membrane are of equal concentrations having equal osmotic pressures (*i.e.*, they are **isotonic**).

Plant Cells as Osmotic Systems. Living cells in plants form osmotic systems due to the presence of semi-permeable **plasma-membrane** and the **cell sap** having a certain osmotic pressure. Plasma-membrane actually is not truly semi-permeable as it allows certain solutes to pass through it and hence, it is known as **selectively permeable** or **differentially permeable** membrane. The **tonoplast** or the **vacuolar membrane** also possesses the same nature. The solvent in case of plants is always **water**. The cell wall is permeable.

If a living plant cell or tissue is placed in water or **hypotonic** solution (whose O.P. is lower than that of cell sap) water enters into the cell sap by osmosis. This process is called as **end-osmosis**. As a result of entry of the water into the cell sap a pressure is developed which presses the protoplasm against the cell wall and the cell becomes **turgid**. This pressure is called as **turgor pressure**. Consequence of the turgor pressure is the **wall pressure** which is exerted by the elastic cell wall against the expanding protoplasm. At a given time turgor pressure (T.P.) equals the wall pressure (W. P.).

$$\text{T.P.} = \text{W.P.}$$

If on the other hand the plant cell or the tissue is placed in **hypertonic** solution (whose O. P. is higher than that of cell sap) the water comes out of the cell sap into the outer solution and the cell becomes **flaccid**. This process is known as **ex-osmosis**.

Cell or tissue will remain as such in **isotonic** solution.

SIGNIFICANCE OF OSMOSIS IN PLANTS

(1) Large quantities of water are absorbed by roots from the soil by osmosis.

(2) Cell to cell movement of water and other substances dissolved in it involves this process.

(3) Opening and closing of stomata depend upon the turgor pressure of the guard cells.

(4) Due to osmosis the turgidity of the cells and hence the shape or form of their organs is maintained.

(5) The resistance of plants to drought and frost increases with increase in osmotic pressure of their cells.

(6) Turgidity of the cells of the young seedlings allows them to come out of the soil.

PLASMOLYSIS

In normal condition the protoplasm is tightly pressed against the cell wall. If this plant cell or tissue is placed in a **hypertonic solution** water comes out from the cell sap into the outer solution due to **ex-osmosis** and the protoplasm begins to contract from the cell wall. This is called as **incipient plasmolysis**.

If the outer hypertonic solution is very much concentrated in comparison to the cell sap the process of ex-osmosis and contraction

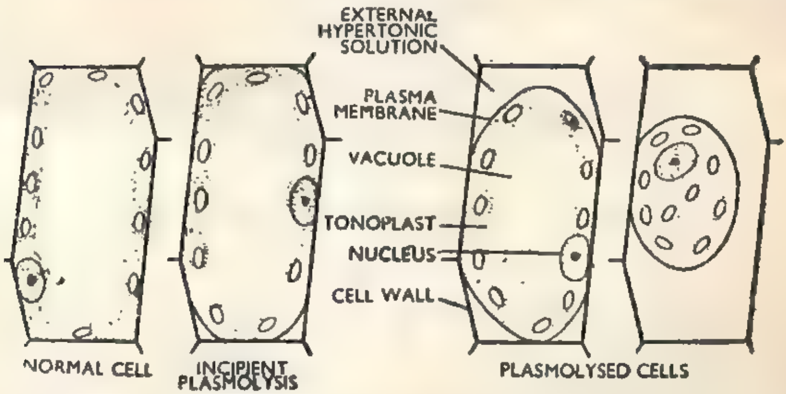


Fig. 2 . Stages in plasmolysis of a plant cell.

or shrinkage of protoplasm continues and ultimately the protoplasm separates from the cell wall and assumes a spherical form. This phenomenon is called as **plasmolysis** and the cell or the tissue is said to be **plasmolysed**. Because of the permeable cell wall the **space** in between the cell wall and plasma-membrane in plasmolysed cell is filled with outer hypertonic solution (Fig. 2)

If a plasmolysed cell or tissue is placed in water, process of **end osmosis** takes place. Water enters into the cell sap, the cell becomes **turgid**, and the protoplasm again assumes its normal shape and position. This phenomenon is called as **deplasmolysis**.

ADVANTAGES OF PLASMOLYSIS

1. It indicates the semi-permeable nature of the plasmamembrane.

2. This phenomenon is ultilized in salting of meat and fishes and addition of concentrated sugar solution to jams and jellies to check the growth of fungi and bacteria which become plasmolysed in conc. solution.

3. It is also used in determining the **O.P.** of the cell sap.

DETERMINATION OF O.P. OF CELL SAP BY PLASMOLYTIC METHOD

This method consists in placing pieces of the plant tissue (the O.P. of whose cell sap is to be measured) in sugar solutions of varying but known concentrations and finding out the particular sugar solution that causes **incipient plasmolysis**. The **O.P.** of the cell sap will be **approximately equal** to the **O.P.** of this sugar solution which is then known from any standard table.

(In fact, the O.P. of the cell sap measured in this way is slightly higher because the sugar solution causing incipient plasmolysis will not be exactly isotonic but slightly hypertonic).

DIFFUSION PRESSURE DEFICIT (D.P.D.) (SUCTION PRESSURE)

Diffusion pressure of a solution is always lower than its pure solvent. The difference between the diffusion pressure of the solution and its solvent at a particular temp. and atm, conditions is called as **Diffusion Pressure Deficit (D.P.D.)**. If the solution is more concentrated its D.P,D. increases but it decreases with the dilution of the solution.

D.P.D. $\propto$ Conc. of the solution.

In case of plants the cell sap is a watery solution of many inorganic and organic substances; *i.e.*, its pure solvent is water. If these cells are placed in pure water the water will enter into the cells due to **higher D.P.D.** of the cell sap or **water deficit**.

In other words, the **D.P.D.** of the cell sap or the cells is a measure of the ability of the cells to absorb water and hence it is

often called as the **Suction Pressure (S.P.)**. It is related with osmotic pressure (**O.P.**) and turgor pressure (**T.P.**) of the cell sap and also the wall pressure (**W.P.**) as follows :

$$\text{D.P.D. (S.P.)} = \text{O.P.} - \text{W.P.}$$

but

$$\text{W.P.} = \text{T.P.}$$

therefore

$$\text{D.P.D. (S.P.)} = \text{O.P.} - \text{T.P.}$$

Due to the entry of the water the osmotic pressure of the cell sap decreases while its turgor pressure is increased so much so that in a **fully turgid cell** turgor pressure equals the osmotic pressure :

$$\text{O.P.} = \text{T.P.} \text{ (in fully turgid cell)}$$

and hence,

$$\text{D.P.D. (S.P.)} = 0$$

On the other hand, the removal of water from the cell sap (ex-osmosis) results in an increase of its **O.P.** and decrease of the turgor pressure so much so that in fully **plasmolysed cells** the value of turgor pressure becomes zero.

$$\text{T.P.} - 0 \text{ (in fully plasmolysed cell)}$$

and hence,

$$\text{S.P.} \quad \text{O.P.}$$

In case, the cell is placed in a **hypotonic solution** instead of pure water, the suction pressure of the cell sap will be :

$$\text{S.P.} = (\text{O.P.} - \text{O.P.}_1) - \text{T.P.}$$

where O.P._1 is the osmotic pressure of outer hypotonic solution.

Thus it is quite obvious that the **D.P.D.** or **S.P.** in case of plant cells is not directly proportional to their osmotic pressure or the concentration of the cell sap but depends both on **O.P.** and **T.P** Higher osmotic pressure of the cell sap is usually accompanied by lower turgor pressure so that its **D.P.D.** or **S.P.** is greater and water enters into it (Fig. 3. A). But, sometimes it is possible that two cells are in contact with each other one having higher osmotic pressure and also higher turgor pressure than the other cell (Fig. 3. B), and still it does not draw water. It is because of its lower **D.P.D.** or **Suction pressure (S.P.)**, no matter its **O.P.** is higher.

Cell a	Cell b
O.P.=25 atm T.P.=15 atm	O.P.=30 atm T.P.=10 atm
S.P.=10 atm	S.P.=20 atm

A

Cell a	Cell b
O.P.=35 atm T.P.=10 atm	O.P.=40 atm T.P.=20 atm
S.P.=25 a m	S.P.=20 atm

B

Fig 3. Entry of water into the cell depends on D.P.D. or Suction Pressure and not on O.P. only.

DETERMINATION OF D.P.D. OR SUCTION PRESSURE

A number of cylinders of tissues (2 or 3 cm. long) are cut from a large sized potato tuber or beet root etc. with the help of the cork-borer after the skin of the potato tuber etc. has been removed. The cylinders of tissue are weighed and placed in different test tubes containing sugar solution of varying but known concentrations (*e.g.*, ·50M, ·45M, ·40M and so on). The test tubes (each of which contains one cylinder of tissue) are plugged.

After about 24 hours, the cylinders of tissue are taken out of the sugar solutions from the test tubes, dried with filter paper, and again weighed. The sugar solution in which the weight of the cylinder of tissue does not change is noted. **D.P.D.** or the Suction Pressure of the tissue will be equal to the osmotic pressure of this sugar solution which can be known from any standard table.

CONCEPT OF WATER POTENTIAL AND OSMOTIC RELATIONS OF PLANT CELLS

According to thermodynamic laws every component of a system possesses **free energy** capable of doing work under constant tempera-

ture conditions. Osmotic movement of water involves certain work done and in fact the main driving force behind this movement is the difference between free energies of water on two sides of the semi-permeable membrane. For nonelectrolytes, free energy/mol. is known as **chemical potential** (denoted by Greek letter psi, ψ). With reference to water this is called as **water potential**.

Like other substances, the absolute value of water potential cannot be determined and measured, instead this value for **pure water** is arbitrarily fixed as zero at one atmosphere and a particular temperature. However, deviations from this value can be ascertained. Although water potential can be expressed in energy terms (ergs/mol.), it is usually expressed in pressure units such as **bars** or **atmospheres** (1 bar $= 10^6$ dynes/sq. cm. or 0·987 atmospheres).

Water potential is lowered by the addition of solutes and because water potential value is zero for pure water, all other water potential values will be **negative**. In other words, the movement of water will take place in osmotic or other systems from a region of **higher water potential** (less negative) to a region of **lower water potential** (more negative).

Osmotic pressure (**O.P.**) in a solution results due to the presence of solutes and the latter lower the water potential (as mentioned earlier). Therefore, osmotic pressure is a quantitative index of the lowering of water potential in a solution and using thermodynamic terminology is called as **osmotic potential** (ψ_s) Osmotic pressure and osmotic potential values are numerically equal but while the former has positive sign, the latter carries a negative sign. If OP$=20$ atms. then, $\psi_s = -20$ atms).

In an open osmotic system, the water potenial and the osmotic potential values are numerically similar and also have same sign (similar will be the case in plasmolysed cells). On the other hand, in a closed osmotic system *e.g.*, in plant cells a pressure is imposed on water which increases the water potential. In plants this pressure is called as **turgor pressure**. This is the actual pressure with positive sign and ranges between zero and numerical osmotic potential value. The potential created by such pressures is called as **pressure potential** ψ_p). Thus in such cases water potential is equal to osmotic potential plus pressure potential.

$$(\psi_w = \psi_s + \psi_p).$$

Summarisingly, it is more appropriate to say that osmotic entry of water into a cell depends on its lower water potential than the outer solution or other cell, instead of saying that it is due to its higher D.P.D. (diffusion pressure deficit). Water potential values of plant cells under different osmotic conditions are given below (see also Fig. 4).

$\psi_w = \psi_s$ (as $\psi_p =$nil)..............in plasmolysed or flaccid
(lowest) cell.

$\psi_w = \psi_s + \psi_p$ ....in partially turgid cell
(higher)

ψ_w = zero (as ψ_p numerically...in fully turgid cell.
(highest) equals ψ_s but both having opposite signs).

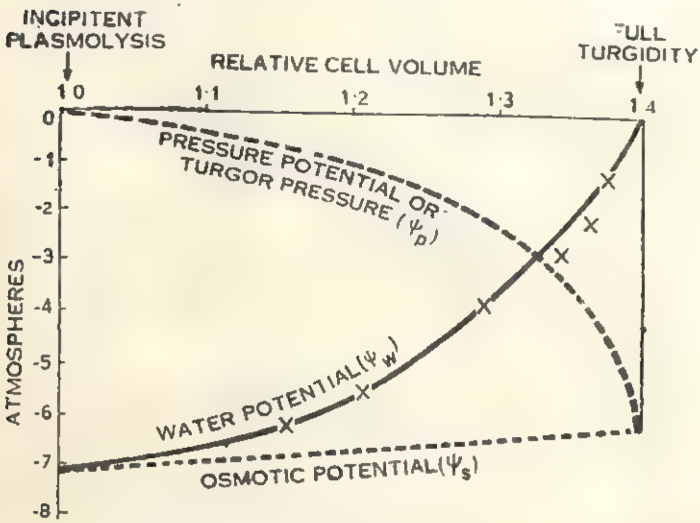


Fig. 4 . Relationship between water potential (ψ_w), osmotic potential (ψ_s) pressure potential or turgor pressure (ψ_p) and cell volume of a plant cell.

2

Absorption of Water

MECHANISM OF ABSORPTION OF WATER

In higher plants water is absorbed through **root hairs** which are in contact with soil water and form a **root hair zone** a little behind the root tips (Fig. 5). Root hairs are tubular hair like prolongations of the cells of the epidermal layer (when epidermis bears root hairs it is also known as piliferous layer) of the roots. The walls of root hairs are **permeable** and consist of **pectic substances** and **cellulose** which are strongly **hydrophilic** (water loving) in nature. Root hairs contain **vacuoles** filled with **cell sap**.

When roots elongate the older hairs die and new root hairs are developed so that they are incontact with fresh supplies of water in the soil.

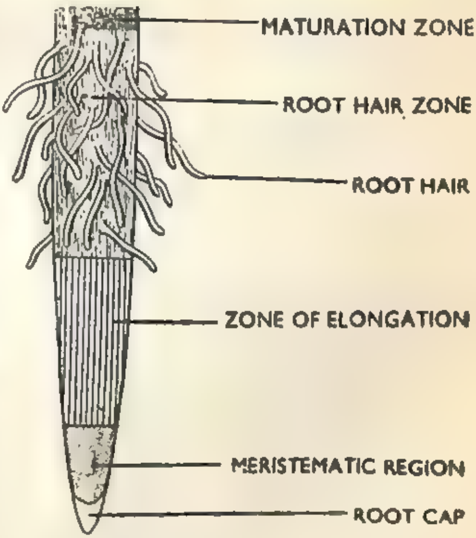


Fig. 5. Diagrammatic representation of a root tip showing root hair zone.

Mechanism of water absorption is of two types :

(1) **Active Absorption of Water.** In this process the root cells play active role in the absorption of water and **metabolic energy** released through respiration is consumed. Active absorption may be of two kinds :—

(a) **Osomotic absorption** *i.e.*, when water is absorbed from the soil into the xylem of the roots according to the **osmotic gradient**.

(b) **Non-osmotic absorption** *i.e.*, when water is absorbed **against** the osmotic gradient.

(2) **Passive absorption of water.** It is mainly due to transpiration, the root cells do not play active role and remain passive.

(1a.) ACTIVE OSMOTIC ABSORPTION OF WATER

First step in the osmotic absorption of water is the **imbibition** of soil water by the hydrophilic cell walls of root hairs.

Osmotic Pressure (O.P.) of the **cell-sap** of root hairs is usually higher than the **O.P.** of the soil water. Therefore, the Diffusion Pressure Deficit (**D.P,D.**) and the suction pressure in the root hairs become higher and water from the cell walls enters into them through **plasma-membrane** (semi-permeable) by **osmotic diffusion.** As a result, the **O.P.**, suction pressure and **D.P.D** of root hairs now become lower, while their **turgor pressure** is increased.

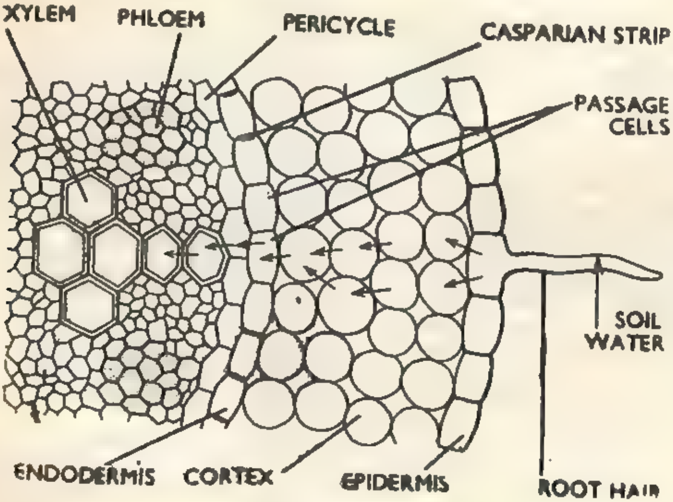


Fig. 6. A par of T.S. of a typical dicot roo . The arrows indicate the pa h of wa er.

Now, the cortical cells adjacent to root hairs have higher **O.P.**, suction pressure and **D.P.D.** in comparison to the root hairs. Therefore, water is drawn into the adjacent cortical cells from the root-hairs by osmotic diffusion.

In the same way, the water by cell to cell osmotic diffusion gradually reaches the innermost cortical cells and the **endodermis**.

Osmotic diffusion of water into endodermis takes place through special thin walled **passage cells** because the other endodermal cells have **casparian strips** on their walls which are impervious to water (Fig. 6).

Water from endodermal cells is drawn into the cells of **pericycle** by osmotic diffusion which now become turgid and their suction pressure is decreased.

In the last step, water is drawn into xylem from turgid pericycle cells. (In roots the vascular bundles are radial and protoxylem elements are in contact with pericycle). It is because in absence of turgor pressure of the xylem vessels (which are non-elastic), the suction pressure of xylem vessels becomes higher than the suction pressure of the cells of the pericycle.

When water enters into xylem from pericycle, a pressure is developed in the xylem of roots which can raise the water to a certain height in the xylem. This pressure is called as **Root Pressure**.

(1b.) ACTIVE NON-OSMOTIC ABSORPTION OF WATER

Sometimes, it has been observed that absorption of water takes place even when the **O.P.** of the soil water is higher than the **O.P.** of cell-sap. This type of absorption which is non-osmotic and against the osmotic gradient requires the expenditure of metabolic energy probably through respiration. Following evidences support this view :

(*i*) the factors which inhibit respiration also decrease water absorption.

(*ii*) poisons which retard metabolic activities of the root cells also retard water absorption.

(*iii*) **auxins** (growth hormones) which increase metabolic activities of the cells stimulate absorption of water.

(2) PASSIVE ABSORPTION OF WATER

Passive absorption of water takes place when rate of transpiration is usually high. Rapid evaporation of water from the leaves during transpiration creates a **tension** in water in the xylem of the leaves. (For details see Chapter 4). This tension is **transmitted** to water in xylem of roots through the xylem of stem and the water rises upward to reach the transpiring surfaces. As a result, soil water enters into the cortical cells through root hairs to reach the xylem of the roots to maintain the supply of water. The force for

this entry of water is created in leaves due to rapid transpiration and hence, the root cells remain passive during this process.

EXTERNAL FACTORS AFFECTING ABSORPTION OF WATER

1. Available Soil Water

Sufficient amount of water should be present in the soil in such form which can easily be absorbed by the plants. Usually the plants absorb **capillary-water** *i.e.*, water present in films in between the soil particles. Other forms of water in the soil *e.g.*, hygroscopic water, combined-water, gravitational water etc. are not easily available to plants.

Increased amount of water in the soil beyond a certain limit results in poor aeration of the soil which retards metabolic activities of root cells like respiration and hence, the rate of water absorption is also retarded.

2. Concentration of the Soil Solution

Increased conc. of soil solution (due to the presence of more salts in the soil) results in higher **osmotic pressure**. If the **O.P.** of soil solution will become higher than the O.P. of cell sap in root cells, the water absorption particularly the osmotic absorption of water will be greatly suppressed. Therefore, absorption of water is poor in alkaline soils and marshes.

3. Soil Air

Absorption of water is retarded in poorly aerated soils because in such soils deficiency of O_2 and consequently the accumulation of CO_2 will retard the metabolic activities of the roots like respiration. This also inhibits rapid growth and elongation of the roots so that they are deprived of the fresh supply of water in the soil.

Water logged soils are poorly aerated and hence, are **physiologically dry**. They are not good for absorption of water.

4. Soil Temperature

Increase in soil temperature up to about 30°C favours water absorption. At higher temperatures water absorption is decreased. At low temp. also water absorption decreases so much so that at about 0°C it is almost checked. This is probably because at low temp :

(*i*) the viscosity of water and protoplasm is increased,

(*ii*) permeability of cell membranes is decreased,

(*iii*) metabolic activities of root cells are decreased, and

(*iv*) growth and elongation of roots are checked.

RELATIVE IMPORTANCE OF ACTIVE AND PASSIVE ABSORPTION OF WATER

There are two views regarding the relative importance of active and passive absorption of water in the water economy of plants. Many workers in the past regarded the active absorption of water to be the main mechanism of water absorption and gave very little importance to the passive absorption. But according to **Kramer** (1969) the active absorption of water is of negligible importance in the water economy of most or perhaps all plants. He regards the root pressure and the related phenomena involved in the active absorption of water as mere consequences of salt accumulation in the xylem of different kinds of roots. The salt accumulation produces a difference in water potential which brings about the inward movement of water (osmotic uptake) and development of a pressure in the xylem sap (root pressure).

There are many reasons for regarding the active absorption as unimportant :

(*i*) The volume of exudate from the cut stump is very small in comparison to the volume of water lost in transpiration by the similar intact plants under conditions favourable for transpiration.

(*ii*) Intact transpiring plants can absorb water from more concentrated and drier soil solutions more easily than the similar detopped plants.

(*iii*) No root pressure can be demonstrated in rapidly transpiring plants. Such plants may show even a **negative root pressure** (*i.e.*, if a little water is placed over the cut stump it is absorbed by the latter).

(*iv*) In conifers root pressure has rarely been observed.

It is held by certain workers that though the active absorption is not important quantitatively, it occurs all the time and supplements passive absorption. Two main arguments are against this view. Firstly, during periods of rapid transpiration the salts are removed from the root xylem so that their concentration becomes very low. Under such conditions the osmotic uptake of water can not be expected to occur. Secondly, even if we suppose that the salts are not removed during periods of rapid transpiration, the latter reduces the water potential of the cortical cells in root to such a low level that the osmotic entry of water from cortex to xylem is not possible.

The available evidence suggests that usually the water is pulled passively into the plant through the roots by forces which are developed in the transpiring surfaces of the shoot. But under certain conditions such as warm, moist soil and low rate of transpiration, salts accumulate in xylem of roots resulting in active osmotic absorption of water.

FIELD CAPACITY OR WATER HOLDING CAPACITY OF THE SOIL

After heavy rainfall or irrigation of the soil some water is drained off along the slopes while the rest percolates down in the soil. Out of this latter water some amount of water gradually reaches the water table under the force of gravity (**gravitational water**) while the rest is retained by the soil. This amount of water retained by the soil after the drainage of gravitational water has become very slow is called as **field capacity** or the **water holding capacity of the soil**.

The field capacity is affected by soil profile, soil structure and temperature. For instance, a fine textured soil overlying a coarse textured soil will have a higher field capacity than a uniformly fine textured soil. Similarly, the field capacity increases with decreasing temperature and *vice versa*.

PERMANENT WILTING PERCENTAGE OR WILTING COEFFICIENT

The percentage of the soil water left after the plant growing in that soil has permanently wilted is called as **permanent wilting percentage** or the **wilting coefficient**.

The permanent wilting percentage can be determined by growing the seedlings in small containers under conditions of adequate water supply till they develop several leaves. The soil surface is then covered and the water supply is cut until wilting occurs. The containers are now transferred to a humid chamber. If the plants do not recover, they are considered to be permanently wilted. Otherwise, they are again transferred to normal atmospheric conditions. This process is repeated till they are permanently wilted. The percentage of the soil water is determined at this point after removing the plants from the containers and shaking off as much soil from their roots as possible.

Earlier workers thought permanent wilting percentage to be a **soil moisture constant**. This view has been strongly criticised by

Slatyer (1957) who pointed out that permanent wilting percentage of a soil is dependent on the osmotic characteristics of the plant and is not a soil-moisture constant. Thus, the different plants if grown in the same soil will wilt at different times depending upon their osmotic potential after the water supply to the soil is stopped.

SOIL TEXTURE IN RELATION TO WATER ABSORPTION

The texture of a soil depends upon the proportion of different sized soil particles in that soil and is a very important factor for the absorption of water in plants. Depending upon their diameters the soil particles are classified as below :

Gravel....................	2 m.m. or more
Coarse sand............	2—·2 m.m.
Fine sand.............	·2 —·02 m.m.
Silt.....................	·02—·002 m.m.
Clay....................	below ·002 m.m.

Sandy Soils

Such soils are very rich in sand particles and though well aerated, they have poor water holding capacity. Sandy soils are, therefore, not good for water absorption.

Clayey Soils

These are rich in clay particles and are poorly aerated. Such soils often become water-logged and are, therefore, neither good for water absorption nor for normal growth of the plants.

Loam

Such soils contain almost equal proportion of the different sized soil particles. They are sufficiently aerated and have good water holding capacity. Therefore, they are very good for water absorption and growth. The loam soil in which the proportion of sand is slightly higher is called as **Sandy Loam** while a loam soil in which clay particles predominate, is called as **Clayey Loam**.

VELAMEN

Many epiphytic orchids develop special aerial adventitious roots which can absorb moisture from the atmosphere. For this purpose, a special water absorbing tissue is present around the cortox of such roots which is called as **velamen** (Fig. 7). It consists of thin-walled parenchymatous cells and the moisture absorbed by it is transferred to the root xylem through exodermis, cortex, endodermis and the perciycle.

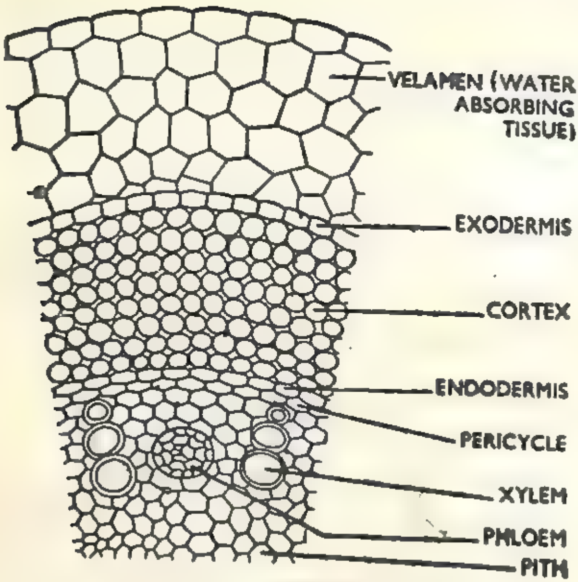


Fig. 7. T.S. of a part of aerial root of an orchid showing velamen.

3

Transpiration and Guttation

TRANSPIRATION

Although large quantities of water are absorbed by plants from the soil but only a small amount of it is utilized. The excess of water is lost from the aerial parts of plants in the form of **water vapours**. This is called as **transpiration**. It can be demonstrated by the following experiment :

A potted plant is kept under bell jar. Before this, the pot is covered in a polythene bag to check the evaporation of water from

Fig. 8. Demonstration of transpiration.

the soil and pot surfaces. The apparatus is made air-tight y apply-

ing some vaseline. After sometime water-drops will be seen on the inner walls of the bell-jar (Fig. 8).

KINDS OF TRANSPIRATION

It is of 3 types :

(1) **Stomatal Transpiration**. Most of the transpiration takes place through stomata. Stomata are usually confined in more numbers on the lower sides of the leaves. In monocots *e. g.* grasses they are equally distributed on all sides. While in aquatic plants with floating leaves they are present on the upper surface.

(2) **Cuticular Transpiration**. Although cuticle is impervious to water, still some water may be lost through it. It may contribute a maximum of about 10% of the total transpiration.

(3) **Lenticular Transpiration**. Some water may be lost by woody stems through **lenticels** which is called as lenticular transpiration.

(transpiration from leaves is called as foliar transpiration)

MECHANISM OF STOMATAL TRANSPIRATION

The mechanism of stomatal transpiration which takes place during the day time can be studied in 3 steps :

(*i*) Osmotic diffusion of water in the leaf from xylem to intercellular spaces above the stomata through the mesophyll cells.

(*ii*) Opening and closing of stomata (stomatal movement), and

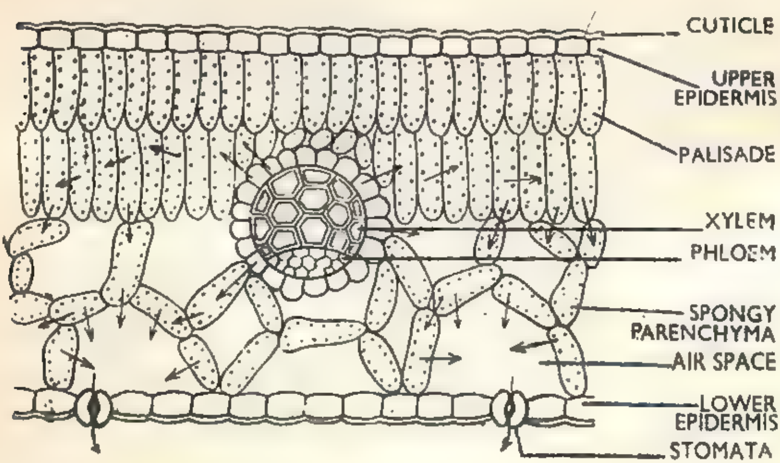


Fig. 9. V.T.S. of a typical dicot leaf. The arrows show the movement of water.

(*iii*) Simple diffusion of water vapours from intercellular spaces to outer atmosphere through stomata.

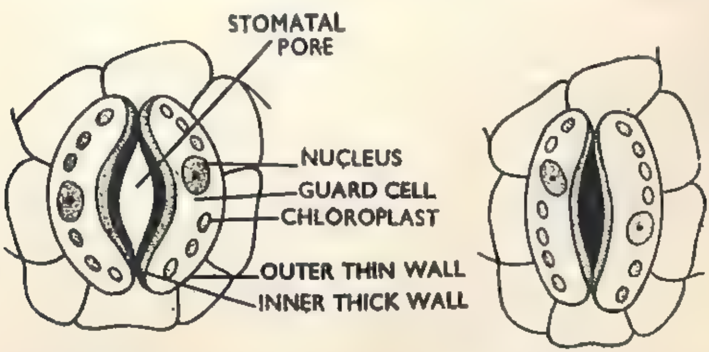
(*i*) Inside the leaf the mesophyll cells are in contact with xylem, and on the other hand with intercellular spaces above the stomata as shown in the Fig. 9. When mesophyll cells draw water from the xylem they become **turgid** and their diffusion pressure deficit (**D.P.D.**) and osmotic pressure (**O.P.**) decrease with the result that they release water in the form of vapours in intercellular spaces close to stomata by osmotic diffusion. Now in turn, the O.P. and D.P.D. of mesophyll cells become higher and hence, they draw water from xylem by osmotic diffusion.

(*ii*) **Opening and Closing of Stomata (Stomatal Movement).**

The inner walls of the guard cells are thick while the outer walls thin and elastic. During night starch accumulates in the guard cells. Because starch is **insoluble** therefore, the **osmotic pressure** of the guard cells is not increased.

In light the insoluble starch is converted into **soluble sugars** in the presence of enzyme *phosphorylase* as follows :

$$\underset{\text{Insoluble}}{\text{Starch}+\text{Inorganic phosphate}} \quad \underset{\substack{\text{Dark} \\ \text{pH 5}}}{\overset{\substack{\text{pH 7} \\ \text{Light}}}{\rightleftharpoons}} \quad \underset{\text{Soluble}}{\text{Glucose}-1-\text{Phosphate}}$$



OPENED STOMATA CLOSED STOMATA

Fig. 10 Opened and closed stomata.

Soluble sugars increase the osmotic pressure of the guard cells, resulting also in an increase of their **D.P.D.** Due to all this, the guard cells draw water from the mesophyll cells by osmotic diffusion

and become **turgid**. The outer thin walls of the guard cells expand while the thick inner walls are stretched thus **opening the stomatal pore** (Fig. 10).

Conversion of starch into sugars is favoured by high temp. and low hydrogen ion concentration (pH abont 7·0). The high pH is probably due to the consumption of CO_2 in light in photosynthesis.

In dark, the soluble sugars are converted back to starch. This lowers the **O.P.** of the guard cells and their **D.P.D.** is also decreased with the result that water is released from the guard cells into the mesophyll cells. Due to this the guard cells become **flaccid**, their thick inner walls come very close to each other so as to **close the stomatal pore** (Fig. 10).

Conversion of sugars into starch is favoured by low temperature and higher hydrogen ion concentration (pH 5). The low pH is probably due to the accumulation of CO_2 in dark.

According to **Steward** (1964) the conversion of starch and inorganic phosphate into glucose—1—phosphate does not cause any appreciable change in the osmotic pressure because the inorganic phosphate and glucose—1—phosphate are equally active osmotically. In his scheme (Fig. 11) he has suggested that (*i*) glucose—1—phosphate should be further converted into glucose and inorganic phosphate for the opening of stomata, and (*ii*) metabolic energy in the form of ATP would be required for the closing of stomata which probably comes through respiration.

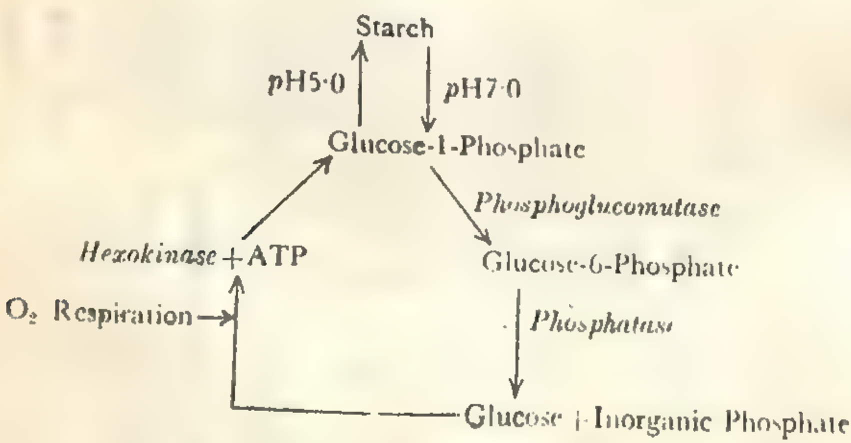


Fig. 11. Steward's scheme of metabolic reactions involved in the opening and closing of stomata.

(the chloroplasts of guard cells are usually non-functional. The starch in guard cells is therefore, derived from the mesophyll tissue)

(*ii*) The last step in the mechanism of transpiration is the **simple diffusion** of water vapours from the intercellular spaces to the outer atmosphere through open stomata. This is because the intercellular spaces are more saturated with moisture in comparison to the outer atmosphere in the vicinity of the stomata.

SIGNIFICANCE OF TRANSPIRATION

Plants waste much of their energy in absorbing large quantities of water, most of which is ultimately to be lost through transpiration. While some people think transpiration as **advantageous** to plant which in fact is not true, others regard it as an **unavoidable process** which is rather harmful.

(A) SUPPOSED ADVANTAGES OF TRANSPIRATION

(1) Supposed Role in the Movement of Water.

Although transpiration plays an important role in the upward movement of water *i.e.*, **ascent of sap** in plants, it does not mean that the translocation of water will be stopped without it. It has been observed that even in the absence of transpiration water continues to rise upward to maintain the turgidity of the cells for various metabolical processes.

(2) Supposed Role in the Absorption and Translocation of Mineral Salts.

Previously, it was thought that more rapid rate of transpiration resulted in an increase in the rate of absorption of mineral salts through increased rate of water absorption. But now it is well established that the absorption of water and absorption of mineral salts are entirely independent processes. Therefore, transpiration has nothing to do with the absorption of mineral salts.

However, once the mineal salts have been absorbed by the plants, their further translocation or distribution may be fascilitated by transpiration through translocation of water in the xylem elements.

(3) Supposed Role in the Regulation of Temperature.

Some of the light energy absorbed by the leaves is utilised in photosynthesis, rest is converted into heat energy which raises their temperature. It has been argued by many workers that traspiration plays an important role in controlling the temperature of the plants. Rapid evaporation of water from the aerial parts of the plant through tarnspiration brings down their temperature and thus prevents them from excessive heating.

But this view is not correct because :—

(*i*) transpiration can not acccount for the total dissipation (loss) of heat energy from leaves and other parts of the plant.

(*ii*) plants kept under intense sun light with their stomata plugged by vaseline do not show much increase in their temperature, and

(*iii*) some xerophytes having structural modifications and adaptations to check excessive transpiration can withstand higher temperatures without appreciable damage to protoplasm.

Dissipation of heat energy from the leaves and other parts of the plant into the outer atmosphere takes place by simple physical processes which in ease of leaves and other objects have also been termed as **thermal emission.**

(B) TRANSPIRATION AS A NECESSARY EVIL

It is quite obvious from the above discussion that transpiration is not of much importance to plants. Besides unnecessary wastage of energy in water absorption due to transpiration, it may be sometimes harmful to them in other respects also. For example :—

(*i*) Very often, when the rate of transpiration is high and soil deficient in water an **internal water deficit** is created in the plants which may affect other metabolic processes.

(*ii*) Many xerophytes have to develop structural modifications and adaptations to check transpiration.

(*iii*) Deciduous trees have to shed their leaves during autumn to check loss of water.

But, inspite of the various disadvantages the **plants can not avoid transpiration** due to their peculiar internal structure particularly those of leaves. Their internal structure although basically meant for gaseous exchange for respiration, photosynthesis etc. is such that it can not check the evaportion of water. Therefore, many workers like **Curtis** (1926) have called transpiration as **necessary evil.**

FACTORS AFFECTING RATE OF TRANSPIRATION

A. EXTERNAL FACTORS

1. Atmospheric Humidity

In **humid** atmosphere (when the Relative Humidity is high) the rate of transpiration **decreases**. It is because the atmosphere is more saturated with moisture and retards the diffusion of water vapours from the intercellular spaces of the leaves to the outer atmosphere through stomata.

In **dry** atmosphere the relative humidity is low and the air not saturated with moisture and hence, the rate of transpiration **increases**.

(Actual amount of moisture content present in the air is the absolute humidity. When it is expressed as a percentage of the total amount of moisture necessary to saturate the air at a particular temperature it is called as Relative Humidity).

2. Temperature

An increase in temperature brings about an increase in the rate of transpiration by

(*i*) lowering the relative humidity, and

(*ii*) opening the stomata widely.

3. Wind

(*i*) When the wind is stagnant (*i.e.*, not blowing) the rate of transpiration remains normal.

(*ii*) When the wind is blowing gently the rate of transpiration increases because it removes moisture from the vicinity of the transpiring parts of the plant, thus facilitating the diffusion of water vapours from the intercellular spaces of the leaves to the outer atmosphere through stomata.

(*iii*) When the wind is blowing violently the rate of transpiration is decreased because it creates hindrance in the outward diffusion of water vapours from the transpiring parts and it may also close the stomata.

4. Atmospheric pressure

Ultimate effect of atmospheric pressure on the rate of transpiration is nil. The positive effect of low atmospheric pressure (*e.g.*, at hills) is neutralised by the low temperature associated with it.

Similarly, the negative effect of high atm. pressure in plains on the rate of transpiration is neutralised by comparatively higher temperature of the plains.

5. Light

Light increases the rate of transpiration because : (*i*) in light stomata open, and (*ii*) it increases the temp.

In dark due to the closure of the stomata, the stomatal transpiration is almost stopped.

6. Available Soil Water

Rate of transpiration will decrease if there is not enough water in the soil in such form which can be easily absorbed by the roots.

B. INTERNAL FACTORS

1. Internal Water Condition

It is very essential for transpiration. Deficiency of water in the plants will result in decrease of transpiration rate. Increased rates of transpiration continuing for longer periods often create **internal water deficit** in plants because absorption of water does not keep pace with it.

2. Structural Features

The number, size, position and the movement of stomata affect rate of transpiration. In dark stomata are closed and stomatal transpiration is checked.

Sunken Stomata help in reducing the rate of stomatal transpiration. When they are situated in grooves and sometimes protected by hairs, the rate of transpiration is further decreased.

In xerophytes the leaves are reduced in size or may even fall to check foliar transpiration.

Thick cuticle or presence of wax coating on exposed parts reduces cuticular transpiration.

DIURNAL FLUCTUATIONS IN THE RATE OF STOMATAL TRANSPIRATION (DAILY PERIODICITY OF TRANSPIRATION)

Stomatal transpiration does not take place at the same rate throughout the daily period of the 24 hours. There are fluctuations (changes) in its rate.

(*i*) In the **morning**, when light falls on plants the stomata begin to open and transpiration starts at a certain rate.

(*ii*) Stomata gradually open widely increasing the rate of transpiration till it reaches its maximum a little **before noon**.

(*iii*) At about **noon**, **internal water deficit** is created because absorption of water fails to keep pace with the rate of transpiration. This lowers the **turgor pressure** of the guard-cells which now become flaccid to close the stomata. Both these factors result in sharp **decline** in the rate of transpiration, (leaves at this stage may even fade out).

(*iv*) Internal water deficit in plants is made good in the **afternoon** gradually due to the absorption of more water by the roots. Stomata again open and the rate of transpiration increases (but is not maximum).

(*v*) In the **evening** the stomata begin to close due to diffused light and the rate of transpiration falls.

(*vi*) At **night** the stomata are closed and the stomatal transpiration is almost completely stopped.

GUTTATION

In some plants such as garden nasturtium, tomato *Colocasia* etc., watery drops ooze out from the uninjured margins of the leaves where a main vein ends. This is called as **guttation** and takes place usually early in the morning when the rate of water absorption and the root pressure are higher while the transpiration is very low. The watery drops consist of water in which many inorganic and organic substances are dissolved. After the drops have dried the salts and organic substances etc., remain in the form of a residue on the margins of the leaves.

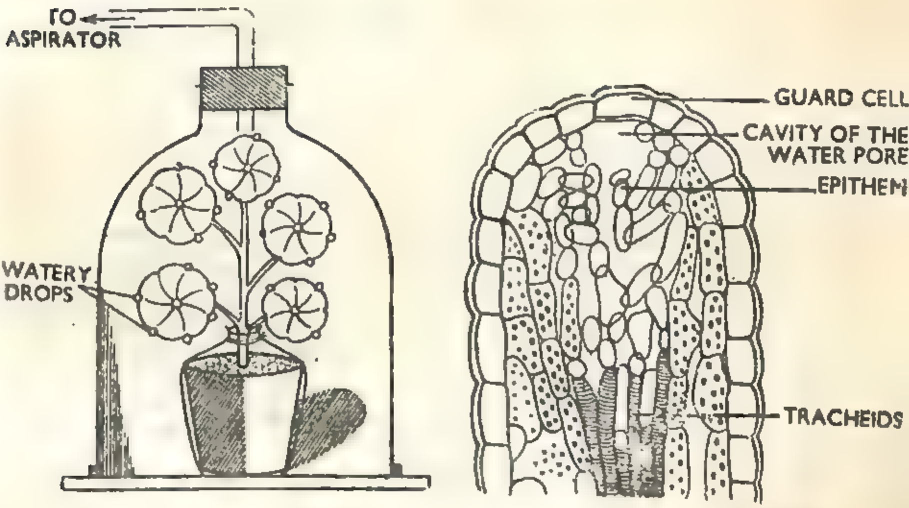


Fig. 12. A. Demonstration of guttation. B. vertical section of a leaf through a hydathode.

The phenomenon of guttation can be demonstrated by a simple experiment (Fig. 12 A). A well watered potted plant of garden nasturtium is kept under a bell-jar on a glass sheet. Before this, the pot is covered in a polythene bag to check the evaporation of water from the soil. The apparatus is made air-tight by applying vaseline. The bell-jar is connected to an aspirator. Air is sucked from the bell-jar by means of the aspirator. After a very short time watery drops will appear on the margins of the leaves.

The phenomenon of guttation is associated with the presence of special types of stomata at the margins of the leaves which are called as **water stomata** or **hydathodes**. Each hydathode consists of a **water pore** which remains permanently open. Below this there is a small **cavity** followed by a loose tissue called as **epithem**. The epithem is in close association with the ends of the vascular elements

of veins (Fig. 12 B). Under higher root pressure the water is given to the epithem by the xylem of the veins. From epithem the water is released into the cavity. When this cavity is completely filled with the watery solution, the latter begins to ooze out in the form of watery drops through the water pore.

4

Ascent of Sap

ASCENT OF SAP

The water after being absorbed by the roots is distributed to all parts of the plant (excess of which is lost through transpiration). In order to reach the topmost parts of the plant, the water has to move upward through the stem. This **upward movement** of water is called as **Ascent of Sap**.

Ascent of sap can be studied under the following two heads : (A) Path of Ascent of Sap, and (B) Mechanism of Ascent of Sap.

(A) PATH OF ASCENT OF SAP

It is well established that the ascent of sap takes place through **xylem**. It can be shown by the following experiments : –

(*i*) A leafy twig of **Balsam** plant (it has semi-transparent stem) is cut under water (to avoid entry of air-bubbles through the cut end) and placed in a beaker containing water with some **eosine** (a dye) dissolved in it. After sometime coloured lines will be seen moving upward in the stem. If sections of stem are cut at this time, only the xylem elements will appear to be filled with coloured water.

(*ii*) **Ringing-Experiment.**

A leafy twig from a tree is cut under water and placed in a beaker filled with water. A **ring of bark** (all the tissues outer to vascular cambium) is removed from the stem. After sometime it is observed that the leaves above the ringed part of the stem remain

fresh and green (Fig. 13). It is because water is being continuously supplied to the upper part of the twig through xylem.

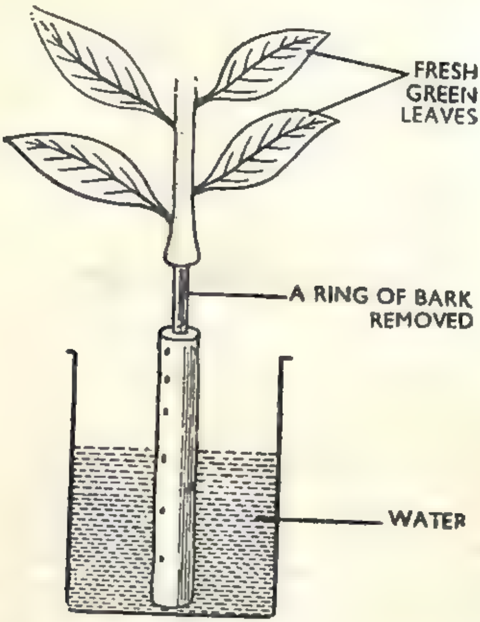


Fig. 13. Ringing Experiment.

(B) MECHANISM OF ASCENT OF SAP

In small trees and harbaceous plants the ascent of sap can be explained easily, but in tall trees like *Eucalyptus*, some conifers such as mighty **Sequoias** (*Sequoia, Sequoiadendron, Metasequoia* are the tallest and thickest trees of the present day flora, sometimes reaching a height of 300-400′) where the water has to rise up to the height of several hundred feet, the ascent of sap, in fact, becomes a problem.

Although the mechanism of ascent of sap is not well understood, a number of theories have been put forward to explain it.

(a) VITAL THEORIES

Supporters of vital theories think that the ascent of sap is under the control of **vital activities** in the stem. Two such theories are common but they are not very convincing :—

(1) According to **Godlewski** (1884) ascent of sap takes place due to the **pumping activity** of the **cells of xylem parenchyma**

which are living. The cells of the **medullary rays** which are also living, in some way change their **O.P.** When their **O.P.** becomes high they draw water from the **lower vessel** and their **O.P.** becomes low. Now due to the low **O.P.**, water from the cells of xylem parenchyma is **pumped** into the **above vessel**. This process is repeated again and again and water rises upward in the xylem.

This theory seemed only hypothetical, and was further discarded by the experiments of **Strasburger**, (1891, 1893) who demonstrated that ascent of sap continues even in the stems in which living cells have been killed by the uptake of poisons.

(2) According to **Bose** (1923) upward translocation of water takes place due to the **pulsatory activity** of living cells of innermost cortical layer just outside the endodermis.

This theory was also rejected because many workers could not repeat his experiment and many other found no correlation between pulsatory activity and the ascent of sap.

(**Bose**, in his experiment used an electric probe which was connected to a galvanometer. When the needle of the electric probe was inserted into the stem slowly and slowly, the needle of the galvanometer showed some oscillations but when the electric probe needle reached the innermost layer of cortex the needle of galvanometer showed violent oscillations. He attributed this to the pulsating activity of these cells.)

(b) ROOT PRESSURE THEORY

Although, **root pressure** which is developed in the xylem of the roots can raise water to a certain height but it does not seem to be an effective force in ascent of sap due to the following points :

(*i*) Magnitude of root pressure is very low (about 2 atms.)

(*ii*) Even in the absence of root pressure, ascent of sap continues. For example, when a leafy twig is cut under water and placed in a beaker full of water it remains fresh and green for sufficient long time.

(*iii*) In gymnosperms root pressure has rarely been observed.

(c) PHYSICAL FORCE THEORIES

Various physical forces may be involved in the ascent of sap :—

(**1**) **Atmospheric Pressure**. This does not seem to be convincing because (i) it can not act on water present in xylem in roots,

(ii) in case it is working, then also it will not be able to raise water beyond 34′.

(2) **Imbibition**. Sachs (1878) supported the view that ascent of sap could take place by imbibition through the walls of xylem. Now it is well known that **imbibitional force** is insignificant in the ascent of sap because it takes place through the **lumen** of xylem elements and not through walls.

(A leafy twig is cut under water and the cut end is dipped in melted paraffin wax for sometime. A thin section of stem near cut end is removed to expose the cell walls. The twig is transferred to a beaker containing water. The twig soon wilts because the lumens of xylem elements have been plugged by wax).

(3) **Capillary Force**. In plants the xylem vessels are placed one above the other forming a sort of continuous channel which can be compared with long capillary tubes and it was thought that as water rises in capillary tube due to capillary force in the same manner ascent of sap takes place in xylem. There are many objections to this theory :—

(*i*) For capillarity a free surface is required.

(*ii*) The magnitude of capillary force is low.

(*iii*) In spring when there is more requirement of water due to the development of new leaves, the wood consists of **broader elements**. While in autumn, when water supply decreases, the wood consists of **narrow elements**. This is against capillarity.

(*iv*) In Gymnosperms usually the vessels are absent. Other xylem elements do not form continuous channels.

(d) TRANSPIRATION PULL AND COHESION OF WATER THEORY

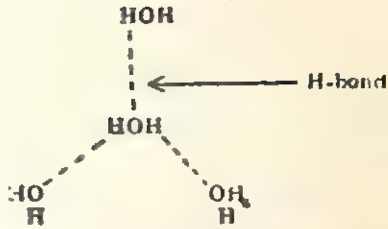
This theory was originally proposed by **Dixon** and **Jolly** (1894) and greatly supported and elaborated by Dixon (1914, 1924). This theory is very convincing and has now been widely supported by many workers. It is based on the followiug features :—

(i) **Cohesive** and **Adhesive** properties of water molecules to form a continuous water column in the xylem.

(ii) **Transpiration pull** exerted on this water column.

Water molecules remain joined to each other due to the presence of **H-bonds** between them.

(Whenever a H-atom comes between two electro-negative atoms a bond is established between the two which is called as H bond and is represented by dotted lines. In case of water the electropositive H-atoms of one water molecule are connected with electronegative O-atoms of other water molecules by H-bonds).



H-bonds between water molecules,

Although H-bond is very weak (containing about 5k. cal. energy) but when they are present in enormous numbers as in case of water, a very strong mutual force of attraction or **cohesive** force develops between water molecules and hence they remain in the form of a **continuous water column** in the xylem. The magnitude of this force is very high (sometimes up to 350 atms), therefore, the continuous water column in the xylem can not be broken easily due to the force of gravity or other obstructions offered by the internal tissues in the upward movement of water.

The **adhesive** properties of water *i.e.*, the attraction between the water molecules and the container's walls (here the walls of xylem) further ensure the continuity of water column in xylem.

When **transpiration** takes place in leaves at the upper parts of the plant, water evaporates from the intercellular spaces of the leaves to the outer atmosphere through the stomata. More water is released into the intercellular spaces from the mesophyll cells. In turn, the mesophyll cells draw water from the xylem of the leaf. Due to all this, a **tension** is created in water in the xylem elements of the leaves. This tension is **transmitted** downward to water in xylem elements of the roots through the xylem of petiole and stem and the water is **pulled** upward in the form of continuous unbroken **water column** to reach the transpiring surfaces—up to the top of the plants.

According to some workers, the main objection against this theory is that certain air bubbles present in the conducting channels will break the continuity of the water column. This has been counteracted by others who say that there are no air bubbles and if at all they are present, they will not break the water column which will remain continuous through other elements of the xylem.

5

Absorption of Mineral Salts

MECHANISM OF MINERAL SALT ABSORPTION

Previously, it was thought that the absorption of mineral salts from the soil took place along with the absorption of water but it is now well established that the mineral salt absorption and water absorption are two different independent processes.

Mineral salts are absorbed from the soil solution in the form of **ions**. They are chiefly absorbed through the **meristematic regions** of the roots near the tips.

Plasma membrane of the root cells is not permeable to all the ions. It is **selectively permeable**. All the ions of the same salt are not absorbed at equal rate but there is **unequal absorption of ions**.

First step in the absorption of mineral salts is the process of **Ion-Exchange** which does not require metabolical energy but greatly facilitates mineral salt absorption.

ION-EXCHANGE

The ions **adsorbed** on the surface of the walls or membranes of root cells may be exchanged with the ions of same sign from external soil solution. For example, the cation $\mathbf{K^+}$ of the external soil solution may be exchanged with $\mathbf{H^+}$ ion adsorbed on the surface of the root cells. Similarly, an anion may be exchanged with $\mathbf{OH^-}$ ion. There are two theories regarding the mechanism of ion-exchange :

(*i*) **Contact Exchange Theory.**

According to this theory the ions adsorbed on the surface of root cells and clay particles (or clay micelles) are not held tightly but oscillate within small volume of space. If the roots and clay

particles are in **close contact** with each other, the oscillation volume of ions adsorbed on root-surface **may** overlap **the** oscillation **vol.** of ions adsorbed on clay particles, and the ions adsorbed on clay particle may be exchanged with the ions adsorbed on root-surface **directly without first being dissolved in soil solution** (Fig. 14 A).

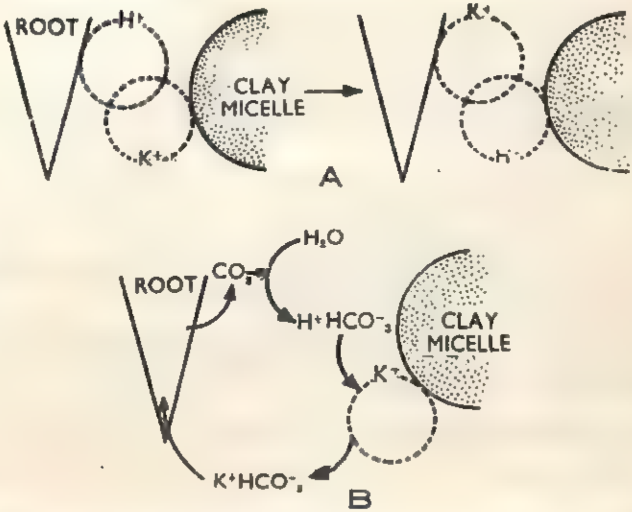


Fig. 14. Diagrammatic representation of (A) the contact-exchange theory and (B) the carbonic acid exchange theory.

(*ii*) **Carbonic Acid Exchange Theory**.

According to this theory, the CO_2 released during respiration of root cells combines with water to form **carbonic acid** (H_2CO_3). Carbonic acid dissociates into $\mathbf{H^+}$ and an anion $\mathbf{HCO_3^-}$ in soil solution. These $\mathbf{H^+}$ ions may be exchanged for cations adsorbed on clay particles. The cations thus released into the soil solution from the clay particles, may be adsorbed on root cells in exchange for $\mathbf{H^+}$ ions or as ion pairs with bicarbonate (Fig. 14 B). Thus, soil solution plays an important role in carbonic acid exchange theory.

The further process of the absorption of mineral salts may be of two types :

(1) Passive and (2) Active.

(1) PASSIVE ABSORPTION OF MINERAL SALTS

When the concentration of mineral salts is higher in the outer solution than in the cell sap of the root cells, the mineral salts are absorbed according to the concentration gradient by simple process of **diffusion**. This is called as **passive absorption** because it does not require expenditure of metabolic energy.

(2) ACTIVE ABSORPTION OF MINERAL SALTS

It has often been observed that the cell sap in plants accumulates large quantities of mineral salts ions **against the concentration gradient**. For example in alga *Nitella* the cell sap accumulated K^+ and phosphate ions to such an extent that their concentrations were thousands and hundreds times greater than in the pond water in which the plant was growing.

This can not be explained by simple diffusion or Donnan's Equilibrium (see page 39) and has led people to believe that absorption and accumulation of mineral salts against the concentration gradient is an **active process** which involves the **expenditure of metabolic energy** through respiration. Following evidences favour this view :

(*i*) the factors like low temp., deficiency of O_2, metabolic inhibitors etc. which inhibit metabolic activities like respiration in plants also inhibit accumulation of ions.

(*ii*) rate of respiration is increased when a plant is transferred from water to salt solution (Salt Respiration).

It has now been accepted that active absorption of mineral salts involves the operation of a **carrier compound** present in the plasma membrane of the cells.

THE CARRIER CONCEPT

According to this theory the plasma membrane is imperme-

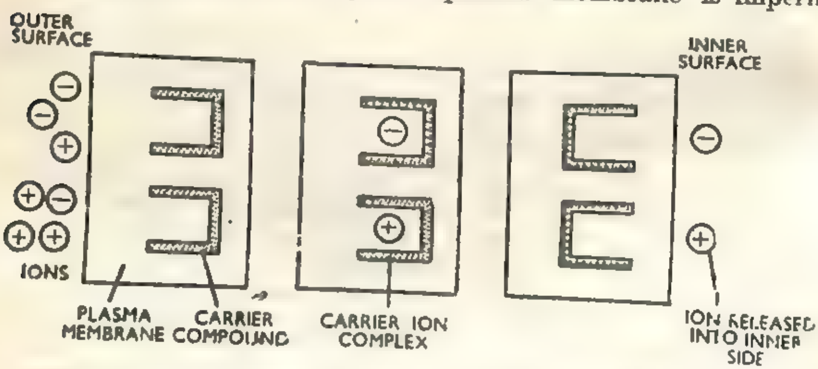


Fig. 15. Diagrammatic representation of a model illustrating the carrier concept.

able to free ions. But some compound present in it acts as carrier and combines with ions to form **carrier-ion-complex** which can move across the membrane. On the inner surface of the membrane this complex breaks releasing ions into the cell while the carrier goes back to the outer surface to pick up fresh ions (Fig. 45).

Following observations strongly support the carrier concept of active absorption of mineral salts :

(*i*) **Isotopic Exchange.**

Several times, it has been found that actively absorbed radio-

active ions (such as $S^{35}O_4$) can not diffuse back or be exchanged with other ions in the outer solution indicating thereby that the plasma membrane is not permeable to free ions.

(*ii*) **Saturation Effects.**

Beyond a certain limit, increased concentration of salts in outer solution does not bring about an increase in the rate of mineral salt absorption. It is because the **active sites** on the carrier compound become saturated with ions.

(*iii*) **Specificity.**

Active sites on carrier compound may be specific which can bind only some specific ions. This also explains the selective and unequal absorption of ions by the plants.

There are two common hypotheses based on the carrier concept to explain the mechanism of active salt absorption, although they are not universally accepted.

(1) Lundegardhs' Cytochrome Pump Theory

Lundegardh and Burstrom (1933) believed that there was a definite correlation between respiration and anion absorption. Thus when a plant is transferred from water to a salt solution tha rate of respiration increases. This increase in rate of respiration has been called as **anion respiration or salt respiration.**

Later on **Lundegardh** (1950, 54) proposed this theory which is based on the following assumptions :

(*i*) the mechanism of anion and cation absorption is different

(*ii*) anions are absorbed through cytochrome* chain by an active process.

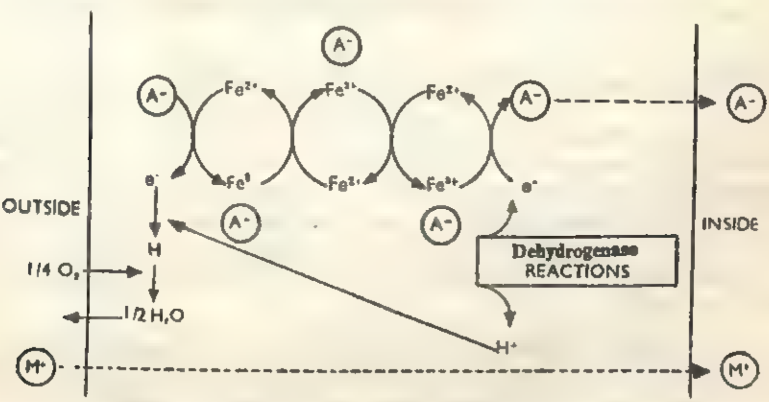


Fig. 16. Diagrammatic representation of the Lundegardh's cytochrome pump theory.

(*Cytochromes are iron-porphyrin proteins that act as enzymes and help in some oxidation-reduction reaction in the cells. These are very important intermediate redox-systems of electron transport chains in chloroplasts and mitochondria transferring electrons from one end of the chain to other along an electrochemical gradient.)

(*iii*) cations are absorbed passively.

According to this theory (Fig. 16), (*i*) **dehydrogenase reactions** on inner side of the membrane give rise to protons (H^+) and electrons (e^-).

(*ii*) The electron travels over the cytochrome chain towards outside the membrane, so that the Fe of the cytochrome becomes reduced (Fe^{++}) on the outer surface and oxidised (Fe^{+++}) on the inner surface.

(*iii*) On the outer surface, the reduced cytochrome is oxidised by oxygen releasing the electron (e^-) and taking an anion (A^-).

(*iv*) The electron thus released unites with H^+ and oxygen to form water.

(*v*) The anion (A^-) travels over the cytochrome chain towards inside.

(*vi*) On the inner surface the oxidised cytochrome becomes reduced by taking an electron produced through the dehydrogenase reactions, and the **anion (A^-) is released**.

(*vii*) As a result of anion absorption, a **cation (M^+) moves passively** from outside to inside to balance the anion.

Main defects of the above theory are :

(*i*) It envisages active absorption of only anions.

(*ii*) It does not explain selective uptake of ions.

(*iii*) It has been found that cations also stimulate respiration.

(2) Bennet-Clark's Protein-Lecithin Theory

In 1956, **Bennet-Clark** suggested that because the cell membranes chiefly consist of phospholipids and proteins and certain enzymes seem to be located on them, the carrier could be a **protein** associated with the phosphatide called as **lecithin**. He also assumed the presence of different phosphatides to correspond with the number of known competitive groups of cations and anions (which will be taken inside the cell).

According to this theory (Fig. 17), (*i*) the phosphate group in the phosphatide is regarded as the active centre binding the cations, and the basic choline group as the anion binding centre.

(*ii*) The ions are liberated on the inner surface of the membrane by decomposition of the lecithin by the enzyme *lecithinase*.

(*iii*) The regeneration of the carrier lecithin from phosphatidic acid and choline takes place in the presence of the enzymes *choline acetylase* and *choline esterase* and **ATP**. The latter acts as a source of energy.

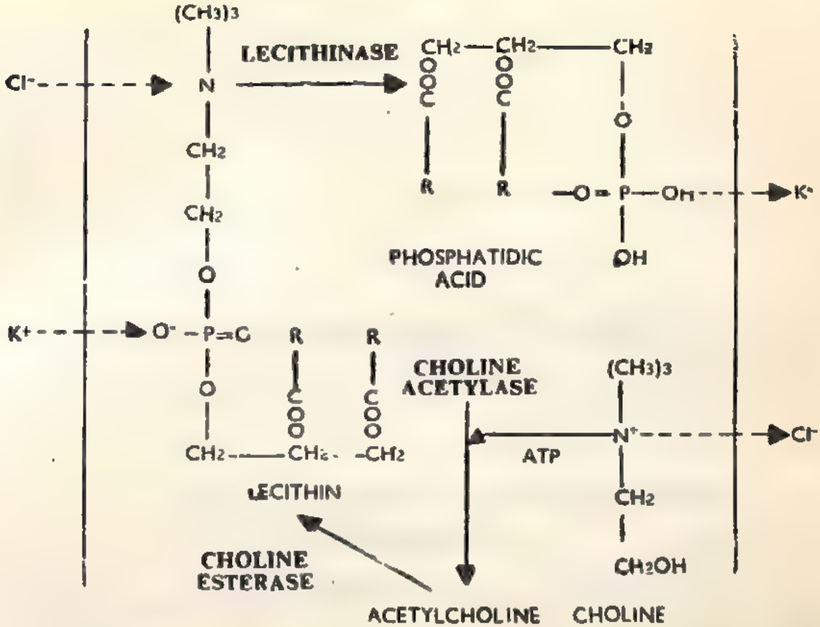


Fig. 17. Diagrammatic representation of the Bennet-Clark's protein-lecithin theory.

DONNAN'S EQUILIBRIUM

The accumulation of ions inside the cells without involving the expenditure of the metabolic energy can be explained to some extent by Donnan's equilibrium theory.

According to this theory there are certain pre-existing ions inside the cell which cannot diffuse outside through membrane. Such ions are called as **indiffusible** or **fixed ions**. However, the membrane is permeable to both anions and cations of the outer solution.

Suppose, there are certain **fixed anions** in the cell which is in contact with the outer solution containing anions and cations. Normally equal number of anions and cations would have diffused into the cell through an electrical potential to balance each other, but to balance the fixed anions more cations will diffuse into the cell. This equilibriuin is known as **Donnan's equilibrium**. In this particular case, there would be an accumulation of cations inside the cell.

If however, there are fixed cations inside the cell, the Donnan's equilibrium will result in an accumulation of anions inside the cell.

6

Mineral Nutrition of Plants

ESSENTIAL AND NON-ESSENTIAL ELEMENTS IN PLANTS

Chemical analysis of the **plant ash** (*i.e.*, the residue left after the dry matter of the plant has been burnt) has shown that plants contain about 40 different elements. Some of them are **indispensible or necessary** for the normal growth and development of the plants and are called as **essential elements**. Rest of the elements are called as **non-essential elements**.

It is now known that the following **15 elements** are **essential** for majority of the plants :—

C, H, O, N, P, K, Ca, S, Mg, Fe, Mn, Zn, B, Cu, and **Mo** (molybdenum). Besides these, **Al, Si, Cl, Na, Co** and **Ga** (gallium) may be essential for some plants.

Essential elements may be classified into two groups :—

(1) MAJOR ELEMENTS (MACRONUTRIENTS)

The essential elements which are required by the plants in comparatively large amounts are called as **major elements** or **macronutrients**. They are :—

C, H, O, N, P, K, Ca, S, Mg, Fe.

(2) MINOR ELEMENTS (OR MICRONUTRIENTS OR TRACE ELEMENTS)

The essential elements which are required in very small amounts or **traces** by the plants are called as **minor elements** or **micronutrients** or **trace elements**. They are :—

Mn, Zn, B, Cu and Mo.

Fe is required in comparatively lesser amounts, therefore, some people consider it as a micronutrient.

(Trace elements should not be confused with the **tracer** elements. Tracer elements are usually radioactive or heavy isotopes which are used to trace out some metabolic pathway).

GENERAL FUNCTIONS OF ESSENTIAL ELEMENTS IN PLANTS

1. Constituents of Protoplasm and Cell Walls.

C, H, O, N, S, and **P** are very important and permanent constituents of the protoplasm and the cell wall. **C, H,** and **O** form most of the part of plant body. **N** is important constituent element of Proteins and Nucleic Acids, **S** of Proteins, and **P** of Nucleic Acids. Besides these, **Mg** is an important constituent of Chlorophylls while **Ca** is present in cell wall in the form of calcium pectate.

2. Influence on the Osmotic Pressure of Plant Cells.

Osmotic pressure and other osmotic relations of the plant cells are maintained due to the presence of organic compounds and mineral salts dissolved in the cell sap.

3. Catalytic Function.

Many elements like **Fe, Cu, Zn, Mo, Mg, Mn, Cl** etc., are required in catalytic amounts to carry on various enzymatic reactions in the cells. These elements may be a part of prosthetic group of the enzymes, or co-enzymes, or may act as activators (for details see Enzymes).

4. Antagonistic or Balancing Function.

Some elements like **Ca, Mg, K** etc., counteract the toxic effects of other mineral elements by maintaining ionic balance.

SPECIFIC ROLES OF ESSENTIAL MINERAL ELEMENTS IN PLANTS

(A) THE MACRONUTRIENTS (MAJOR ELEMENTS)

1. NITROGEN.

Specific Role (Function)

- It is important constituent of proteins, nucleic acids, porphyrins, alkaloids, some vitamins, coenzymes etc.

- Porphyrins are important part of Chlorophylls and Cytochromes.

- Thus it plays very important role in metabolism, growth, reproduction and heredity.

Deficiency Symptoms

- Nitrogen deficiency causes **yellowing** *i.e.*, **chlorosis** of leaves. Older leaves are affected first.
- In many plants *e.g.*, tomato the stem, petiole and the leaf veins become coloured due to the formation of **anthocyanin pigments.**

Plant growth is stunted (because protein content, cell division, and cell-enlargement are decreased).

2. PHOSPHOROUS

Specific Role

- It is important constituent of nucleic acids, phospholipids, coenzyme NAD, NADP and ATP etc.
- Phospholipids along with proteins may be important constituents of cell membranes.
- Through nucleic acids and ATP it plays important role in protein synthesis.
- Through coenzymes NAD, NADP and ATP it plays important role in oxidation reduction and energy transfer reactions of cell metabolism *e.g.*, Photosynthesis, Respiration, Fat metabolism etc.

Deficiency Symptoms

- Phosphorous deficiency may cause premature leaf fall.
- Dead necrotic areas may be developed on leaves or fruits.
- Leaves may turn dark to blue-green in colour.

3. SULPHUR

Specific Role

- It is important constituent of some amino acids (cystine, cysteine and methionine) which with other amino acids form the proteins.
- Disulphide linkages help to stabilize the protein structure.
- It is also constituent of vitamins *biotin*, *thiamine*, and coenzyme A.
- Sulfhydryl groups are necessary for the activity of many enzymes.

Deficiency Symptoms

- Sulphur deficiency causes yellowing (*i.e.*, chlorosis) of the leaves. The younger leaves are affected first.
- Tips and margins of the leaf roll inward
- Stem becomes hard due to the development of sclerenchyma.
- Protein synthesis is inhibited.

4. CALCIUM

Specific Role

- It is important constituent of the middle lamella in cell wall.
- It is essential in the formation of cell membranes.
- It helps to stabilise the structure of the chromosomes.
- It may be an activator for many enzymes.

Deficiency Symptoms

- Calcium deficiency causes disintegration of growing meristematic regions of the roots, stem, and leaves.
- Chlorosis occurs along the margins of the younger leaves.
- Malformation of younger leaves also takes place.

5. MAGNESIUM

Specific Role

- It is very important constituent of Chlorophylls.
- It acts as activator for many enzymes in **phosphate transfer reactions** particularly in carbohydrate metabolism and nucleic acids synthesis.
- It plays important role in binding ribosomal particles during protein synthesis.

Deficiency Symptoms

— Magnesium deficiency causes interveinal chlorosis of the leaves. The older leaves are affected first.

— Dead necrotic patches appear on the leaves.

6. POTASSIUM

Specific Role

- Although potassium is not a constituent of important organic compound in the cells, it is essential for the process of respiration and photosynthesis.
- It probably acts as an activator of many enzymes involved in carbohydrate metabolism and protein synthesis.

Deficiency Symptoms

- Mottled chlorosis of leaves occurs.

— Necrotic areas develop at the tip and margins of the leaf which curve downward.

— Plant growth remains stunted with marked shortening of internodes.

7. IRON

Specific Role

- It is important constituent of iron-porphyrin proteins like cytochromes, peroxidases, catalases etc.
- It is essential for the synthesis of chlorophyll.
- It is very important constituent of **Ferredoxin** which plays important role in **biological nitrogen fixation** and **primary photochemical reaction** in photosynthesis.

Deficiency Symptoms

— Iron deficiency causes rapid chlorosis of the leaves which is usually interveinal.

(B) THE MICRONUTRIENTS (MINOR OR TRACE ELEMENTS)

1. MANGANESE

Specific Role

- It is an activator of many respiratory enzymes.
- It is also activator of the enzymes *Nitrite reductase* and *Hydroxylamine reductase*.
- It is necessary for the evolution of oxygen during photosynthesis.

Deficiency Symptoms

— Manganese deficiency causes chlorotic and necrotic spots in the interveinal areas of the leaf.

2. COPPER

Specific Role

- It is constituent of several oxidising enzymes.
- Its higher concentrations are toxic to plants.

Deficiency Symptoms

— Copper deficiency causes necrosis of the tip of the young leaves.

— It also causes **die-back** of citrus and other fruit trees and **reclamation** disease of cereals and leguminous plants.

3. ZINC

Specific Role

- It is involved in the biosynthesis of the growth hormone *Auxin* Indole-3-Acetic acid (**IAA**).

● It acts as activator of many enzymes like *carbonic anhydrase*, *alcohol-dehydrogenase* etc.

Deficiency Symptoms

—Zinc deficiency causes chlorosis of the older leaves which starts from tips and the margins.

—It causes **mottle leaf** disease in apple, citrus, walnut and other fruit trees.

4. BORON

Specific Role

● Specific role of boron in the metabolism of plants is not clear.

● It probably facilitates the translocation of sugars.

Deficiency Symptoms

—Boron deficiency causes death of the shoot tip.

—Flower formation is suppressed.

—Root growth is stunted.

—Leaves become coppery in texture.

5. MOLYBDENUM

Specific Role

● It is associated with the prosthetic group of the enzyme *nitrate reductase* and thus plays important role in nitrogen metabolism.

Deficiency Symptoms

—Molybdenum deficiency causes chlorotic interveinal mottling of the older leaves.

—Flower formation is inhibited.

Causes **whiptail** disease in cauliflower plants.

DETERMINATION OF ESSENTIALITY OF MINERAL ELEMENTS

The essentiality of a particular mineral element for the normal growth and development of the plant can be determined by **solution culture** method. The roots of the plant which is to be studied are imersed in nutrient solution of known chemical composition containing all the essential mineral elements in a container. The stem of the plant is kept projecting through a hole in the cover of the container.

The stem is projected from the sharp edge of the hole with a pad of non-absorbant cotton. The nutrient solution is aerated for optimum growth of the roots and mineral salt absorption (Fig. 18). The above plant serves as control.

A second similar plant is now fixed in another container in which the nutrient solution lacks a particular mineral element whose essentiality is to be determined. The effect of the deficiency of this mineral element is then observed on the growth of the plant. If the plant deviates from its normal growth *i.e.*, it shows the deficiency symptoms, the mineral element missing from the nutrient solution will be an essential element for the growth and development of the plant.

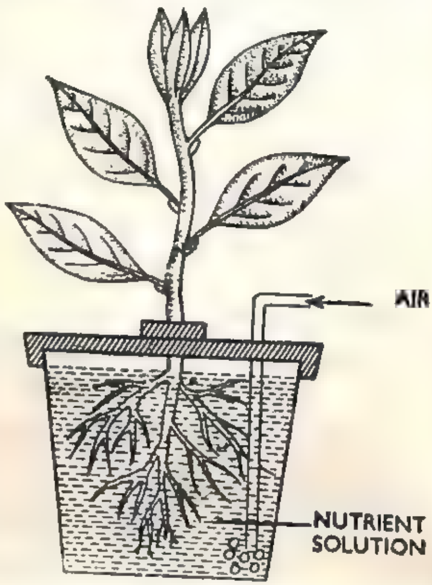


Fig. 18. Solution Culture

Precautions. Great care should be taken to avoid the contamination of the nutrient solution as far as possible particularly with the trace elements. These elements are often present as impurities in (*i*) container's wall (*ii*) water used in preparing the nutrient solution (*iii*) reagents used (*iv*) rooting medium, and (*v*) the dust in surrounding atmosphere.

SOILLESS GROWTH OR HYDROPONICS

The practice of growing plants in nutrient-enriched water without soil is called as **soilless growth** or **hydroponics**. However, the term hydroponics is now being applied to plants rooted in sand, gravel or other similar matter which is soaked with a recycling flow of nutrient-enriched water.

The plants are grown in large tanks containing nutrient solution and are supported by wire netting. The tanks are provided with the solution-regulating and pumping system and are placed in green houses under controlled environment. After about a month in the greenhouse when the plants flower, they are further supported by strings attached to the greenhouse roof. Because the plants are grown in large tanks, this process of soilless cultivation is also known as **tank farming**.

Hydroponics has achieved success in experimental stations around the world and is gradually coming into commercial use in countries like United States, Abu Dhabi etc.

According to a recent **United Nations** report on hydroponics : 'In large areas of the tropics, water deficiency is the limiting factor in crop production, and it is in these regions that the soilless methods hold out much promise because of the more economical use of such water as is available'. The report adds : 'In some areas, lack of fertile soil or very thin soil layers may also make soilless methods worth serious consideration'. Besides these, the other advantages of growing cucumbers, egg plants, peppers, lettuces, spinach and other vegetables hydroponically under controlled environment are (*i*) the regulation of nutrients, (*ii*) control of pests and diseases, (*iii*) reduction of labour cost and (*iv*) sometimes, quicker yield.

But there are two main drawbacks of hydroponics farming. Firstly, the cost of setting up the system is very high. A typical hydroponics unit including the environmental control equipment and which encompasses three-quarters of an acre costs lakhs of rupees. Secondly, it requires skill and knowledge for its operation. The **UN** report says : To make a real success of the method, it is necessary to have some knowledge of plant physiological principles and even of elementary chemistry as well as sound knowledge of how to grow the crop'.

However, the future of growing crops under unfavourable conditions hydroponically seems to be promising.

7

Nitrogen Metabolism

ROLE OF NITROGEN IN PLANTS

Nitrogen is a universally occurring element in all the living beings. Apart from water and mineral salts the next major substance in plant cells is **protein** (about 10-12% of the cell). These proteins which are **building blocks** of the protoplasm are made up of nitrogenous substances called as the **amino acids** which in turn are synthesized when **inorganic nitrogen** of the environment is converted into **organic nitrogen** inside the plants. (Plant cells are therefore unique in their ability to convert inorganic nitrogen into organic nitrogen).

Nitrogen is also constituent element of many other important organic compounds like **chlorophylls**, **Cytochromes**, **alkaloids**, many **vitamins** (which serve as functional groups of many enzymes) and above all of **nucleic acids** and thus plays a very important and fundamental role in metabolism, growth, reproduction, and heredity.

SOURCES OF NITROGEN TO PLANTS

(1) Atmospheric Nitrogen (Molecular Nitrogen)

Although about 80% of the earth's atmosphere is composed of nitrogen, the majority of the plants can not utilise this form of nitrogen. Only **some bacteria, some blue-green algae, leguminous plants** (having root nodules) etc. can fix atmospheric nitrogen.

(2) Nitra , Nitrites, Ammonia in the Soil (Inorganic Nitrogen)

Among these, the **nitrate** is the chief form of nitrogen taken up by the plants from the soil.

(3) Amino Acids (Organic Nitrogen) in the Soil

Many soil micro-organisms make use of this form of nitrogen. Sometimes it may also be taken by higher plants.

(4) Organic Nitrogenous Compounds in Bodies of the Insects

Insectivorous plants fulfil their nitrogen requirement by catching the small insects and digesting them

CONVERSION OF NITRATE INTO AMMONIA BY THE PLANTS

Nitrogen in nitrate (NO_3^-) is present in highly oxidised state while in ammonia in reduced form. Therefore, the conversion of nitrate to ammonia is a **reductive process.**

Reduction of nitrate to ammonia takes place in many steps which are mediated by specific enzymes. At each step **two electrons** are added and ultimately NO_3 in which nitrogen has **5 positive charges** is converted into NH_3 in which nitrogen has **3 negative charges.** The electrons are supplied by reduced coenzyme I *i.e.*, **NADH** (Nicotinamide Adenine Dinucleotide) and reduced coenzyme II *i.e.*, **NADPH** (Nicotinamide Adenine Dinucleotide Phosphate).

$$\underset{\text{Nitrate}}{\overset{+5}{N}O_3} \xrightarrow{2e} \underset{\text{Nitrite}}{\overset{+3}{N}O_2} \xrightarrow{2e} \underset{\text{Hyponitrite}}{H_2\overset{+1}{N_2}O_2\,(?)} \xrightarrow{2e} \underset{\text{Hydroxyl-amine}}{\overset{-1}{N}H_2OH\,(?)} \xrightarrow{2e} \underset{\text{Ammonia}}{\overset{-3}{N}H_3}$$

(1) Reduction of Nitrate to Nitrite

Reduction of nitrate to nitrite takes place in the presence of the enzyme *nitrate reductase* which requires reduced coenzyme I (NADH) or II (NADPH).

$$\underset{\text{nitrate}}{NO_3} + \underset{\text{reduced coenzyme}}{NADH} + H^+ \xrightarrow{\text{Nitrate reductase}} \underset{\text{nitrite}}{NO_2} + \underset{\text{oxi. coenzyme}}{NAD} + H_2O$$

This enzyme which is a **molybdoflavo protein** with an operative sulfhydryl group was first isolated by **Evans** and **Nason** in 1953 from *Neurospora* (a fungus) and Soyabean leaves. The enzyme isolated from *Neurospora* could utilise only reduced coenzyme II (NADPH) while the enzyme isolated from Soyabean leaves could utilise both the reduced coenzyme I (NADH) and II (NADPH).

This enzyme contains FAD (Flavin Adenine Dinucleotide) as its prosthetic group with which is associated **molybdenum (Mo).**

Actual reduction of NO_3 to NO_2 takes place as shown in the Fig. 19.

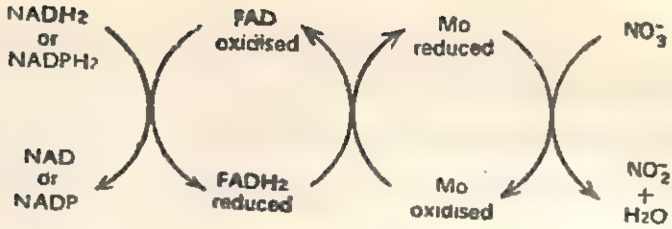


Fig. 19. Reduction of nitrate to nitrire

Electrons are transferred from reduced coenzyme to FAD which becomes reduced (**$FADH_2$**). From reduced **$FADH_2$** the electrons are finally transferred to NO_3^- through **Molybdenum** so that NO_2^- and H_2O are formed.

(Nitrate reduction takes place chiefly in green leaves and roots).

(2) Reduction of Nitrite to Ammonia

It takes place in the presence of the enzyme *nitrite reductase* which requires reduced coenzyme I or II.

$$3NADH + NO_2 + 4H^+ \xrightarrow{\text{Nitrite reductase}} 3NAD + NH_3 + 2H_2O$$

Manganese (Mn) seems to be associated with the prosthetic group of this enzyme which was first isolated by **Nason et al*** from *Neurospora* and Soyabean leaves.

Previously it was thought that the reduction of nitrite to ammonia involved the formation of two **intermediate compounds** *i.e.*, **hyponitrite ($H_2N_2O_2$) and hydroxlamine (NH_2OH)** but it is doubtful because :—

(*i*) Hyponitrite is quite unstable.

(*ii*) Hydroxylamine is toxic.

(*iii*) Moreover, they have never been observed in free state in the cells.

It is now generally believed that hyponitrite and hydroxylamine may at the best be formed at the surface of the enzyme and leave the surface only when they are completely reduced to further inter mediate or ammonia.

*(et al=and collaborators)

BIOLOGICAL NITROGEN FIXATION

Conversion of molecular nitrogen of the atmosphere into inorganic nitrogenous compounds through the agency of some living organisms is called as **biological nitrogen fixation.**

NITROGEN FIXING ORGANISMS

Not all the organisms have capacity to fix the atmospheric nitrogen. Only certain **bacteria**, some **blue-green algae**, and **leguminous plants** etc., can fix atom, nitrogen. They can be grouped as follows :

1. AUTOTROPHIC

(a) **Aerobic** *e.g.*, some blue-green algae. All those blue green algae which can fix atm. nitrogen contain **heterocysts,** but all the heterocyst bearing blue-green algae may not be atm. nitrogen fixers.

(b) **Anaerobic** *e.g.*, *Rhodospisillum*, *Chromatium.*

2. HETEROTROPHIC

(a) **Aerobic** *e.g.*, *Azotobacter.*

(b) **Anaerobic** *e.g. Clostridium.*

3. SYMBIOTIC

Bacterium *Rhizobium leguminosarium* (= *Bacillus radicicola*) associated with the **root nodules** of leguminous plants. None of these two partners alone can fix atm. nitrogen.

Besides the leguminous plants, many other non-legumious plants are known to fix atm. nitrogen. In all such cases some **micro-organism** is present living symbiotically with the higher plants. They are :—

(i) Root Nodules of non-Legume Angiosperms

Many species of as many as 13 genera of non-leguminous angiosperms which are all woody and dicots bear root nodules that can fix nitrogen *e.g.*, *Casuarina, Alnus, Ceanothus, Elaeagnus* etc.

(ii) Root Nodules of Gymnosperms

For example, many members of Cycadaceae, *Podocarpus* etc.

(iii) Mycorrhizal Plants

For example, *Pinus* Mycorrhiza.

(iv) Leaf Nodules

Some members of the family **Rubiaceae** *e.g.*, *Chomelia*, *Pavetta* etc., develop nodule-like structures on the leaves that contain nitrogen fixing bacteria.

(v) Phyllosphere Association

Ruinen (1954, 1961) has observed considerable variety of micro-organisms occuring abundantly on the surface of the leaves of many trees and shrubs under humid tropical conditions and suggested that these organisms might fix nitrogen. The environment provided by the wet leaf surface for microbial development was termed by her as '**phyllosphere**'.

MECHANISM OF BIOLOGICAL NITROGEN FIXATION

(A) NON-SYMBIOTIC NITROGEN FIXATION

Mechanism of the nitrogen fixation remained obscure for a long time. Considerable breakthrough has been made in the understanding of nitrogen-fixation during early sixties by the work of **Shneider et al** (1960), **Carnahan et al** (1960) etc. on **cell-free extracts** of nitrogen fixing bacteria and blue-green algae making ample use of heavy isotope of nitrogen, N^{15}.

Their studies have also shown considerable similarity in bacterial and algal nitrogen fixation, although there are a few significant differences.

It has been concluded that the following ingredients are necessary for nitrogen-fixation in the cell system of **nitrogen fixing bacteria** :—

(1) Presence of *hydrogenase* and *nitrogenase* enzyme systems. *Hydrogenase* reversibly catalyses the reduction of hydrogen ion to molecular hydrogen while *nitrogenase* reduces molecular nitrogen to NH_3 in the presence of molecular hydrogen.

(2) Presence of **Ferredoxin** (a non-heme iron protein) as an electron carrier.

(3) Presence of **Pyruvate** which acts as electron donor and energy source.

(4) Presence of co-factors *viz.*, **TPP** (Thiamine Pyro Phosphate), **coenzyme A** (CoA), inorganic phosphate, and Mg^{++} which seem to be required in the metabolic utilization of pyruvate leading to the formation of energy (**ATP**).

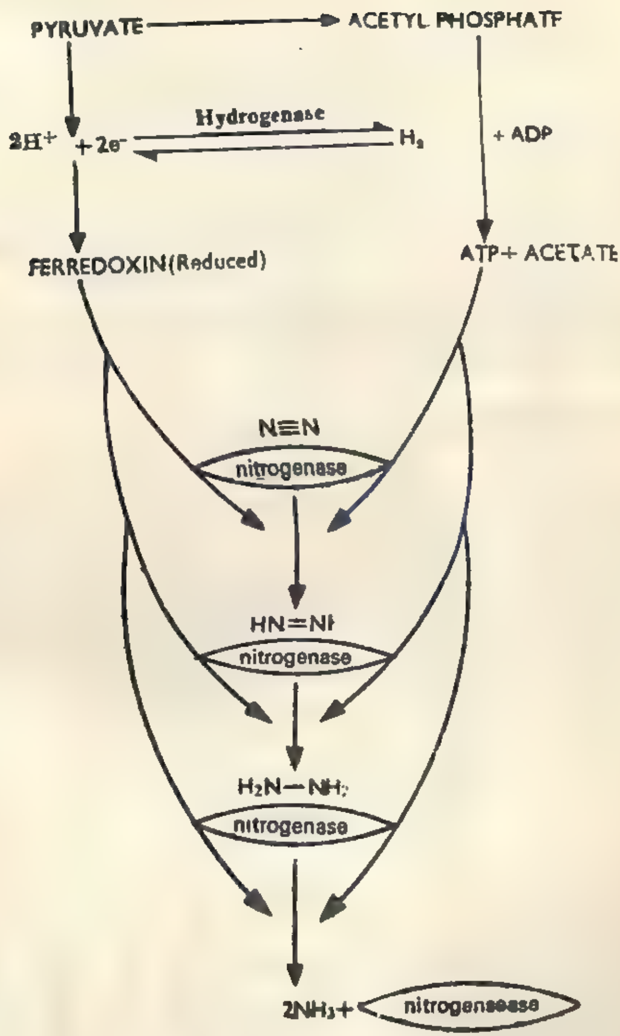


Fig. 20 Burris scheme of atmospheric nitrogen fixation.

According to the scheme of **Burris** (1965) which has been shown in the figure 20, the fixation of nitrogen takes place as follows :—

(i) **Phosphoroclastic** breakdown of pyruvate results in the production **of electrons** and **acetyl phosphate**.

(ii) Ferredoxin accepts electrons coming from pyruvate and gets reduced.

(iii) Acetyl phosphate reacts with **ADP** to generate energy **(ATP)**.

(iv) In the presence of the reduced ferredoxin and ATP, molecular nitrogen is absorbed on the surface of the enzyme *nitrogenase.*

(v) Electrons are now transferred to N_2.

(vi) Reduction of nitrogen takes place and the enzyme is set free only when nitrogen has been completely reduced to **ammonia (NH_3)**.

It is thought that in photosynthetic bacteria like *Chromatium* and blue-green algae which can fix nitrogen, the electrons and energy (ATP) are provided by photosynthesis.

(B) SYMBIOTIC NITROGEN FIXATION

The mechanism of symbiotic nitrogen fixation has been studied in comparatively less detail than in case of bacteria. According to the recent view the action of the enzyme *nitrogenase* is based on **electron activation two-site hypothesis**. There are two active sites on this enzyme. At first, electrons reduce a group **X** to **XH** at the first active site in the presence of ATP. Probably molybdenum is associated here. At the second active site nitrogen is attached to a group **Y** which also involves a metal probably Fe^{++} Then two electron reduction takes place step by step forming **diimide** and **hydrazine** as intermediates which remain attached to the enzyme. Finally, hydrazine enzyme complex is splitted. **XNH_2** and **YNH_2** produce two molecules of **NH_3**. The groups X and Y again become free.

In root nodules of leguminous plants a red pigment which is very much similar to the hemoglobin of the red blood corpuscles is found. This pigment is called as **leghemoglobin** and appears to be a product of *Rhizobium*-legume complex. Although a correlation has been found between the conc. of leghemoglobin and the rate of nitrogen fixation, this pigment does not play a direct role in nitrogen fixation. It probably (i) maintains the low oxygen tension required for nitrogen fixation and (ii) even at very low level of O_2 it maintains the supply of the latter to Rhizobia.

Formation of Root Nodules in Leguminous Plants.

The **Rhizobia** accumulate in the soil near the roots of the legumes probably due to the secretion of some growth factors by their roots. The bacteria now penetrate the roots through soft or injured root hairs whose tips become curved. They now enter into the cells of the inner layers of the cortex through infection thread and cause cortical cells to multiply which ultimately result in the

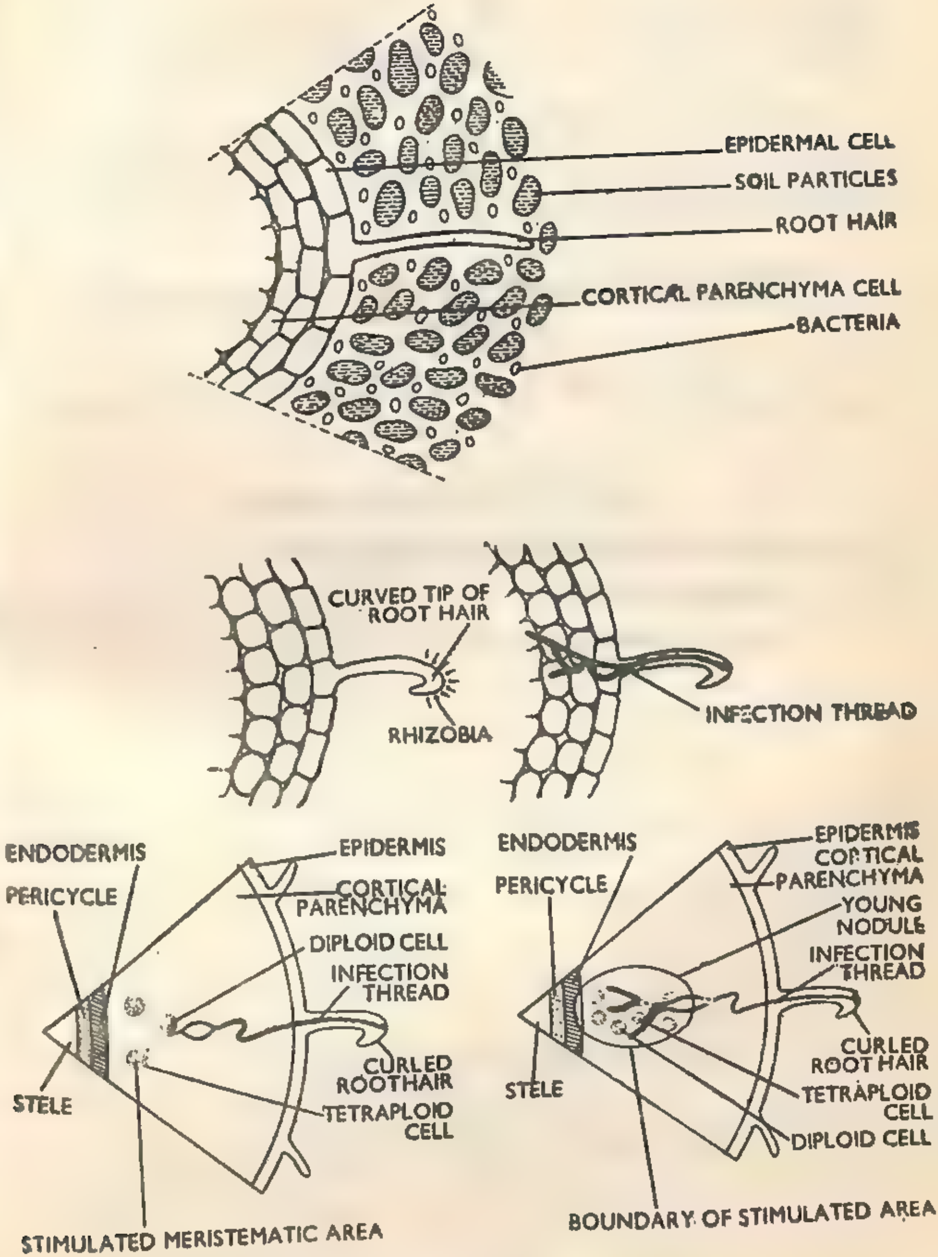


Fig. 21. Penetration of the *Rhizobia* into the root hair of a leguminous plant and formation of root nodule.

formation of nodules on the surface of the roots (Fig. 21). Recent electron microscopic studies have shown groups of Rhizobia to be surrounded by double membranes. The latter probably originates from the host cell wall.

The number of chromosomes in cortical cells infected by **Rhizobia** which later develop into nodule is double the number of chromosomes in other somatic cells of the legume and seems to be a prerequisite for nodule formation.

AMINO ACIDS CONSTITUTING THE PROTEINS IN PLANTS

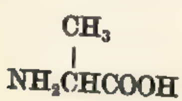
Plant proteins consist of over 20 different types of amino acids which are as follow :

1. ALIPHATIC AMINO ACIDS

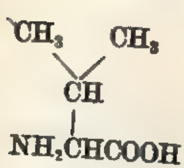
(a) Monoamino Monocarboxylic Amino Acids.

I. NH_2CH_2COOH

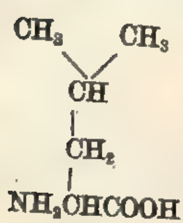
Glycine (amino acetic acid)

2. 

Alanine (α-amino propionic acid)

3. 

Valine (α-amino isovaleric acid)

4. 

Leucine (α-amino isocaproic acid)

5.

$$\begin{array}{l} \quad CH_3 \\ \quad | \\ \quad CH_2 \\ \quad | \\ \quad CHCH_3 \\ \quad | \\ NH_2CHCOOH \end{array}$$

Isoleucine (α-amino, β-methyl valeric acid)

6.

$$\begin{array}{l} \quad CH_2OH \\ \quad | \\ NH_2CHCOOH \end{array}$$

Serine (α-amino, β-hydroxyl propionic acid)

7.

$$\begin{array}{l} \quad CH_3 \\ \quad | \\ \quad HCOH \\ \quad | \\ NH_2CHCOOH \end{array}$$

Threonine (α-amino, β-hydroxyl butyric acid)

(b) Sulphur Containing Amino Acids)

8.

$$\begin{array}{l} \quad CH_2SH \\ \quad | \\ NH_2CHCOOH \end{array}$$

Cysteine (α-amino, β-mercapto propionic acid)

9.

$$\begin{array}{lcl} CH_2-S & — & S-CH_2 \\ | & & | \\ NH_2CHCOOH & & NH_2CHCOOH \end{array}$$

Cystine

10.

$$\begin{array}{l} \quad SCH_3 \\ \quad | \\ \quad CH_2 \\ \quad | \\ \quad CH_2 \\ \quad | \\ NH_2CHCOOH \end{array}$$

Methionine

(c) Monoamino Dicarboxylic Amino Acids and Their Amides (Acidic Amino Acids)

11.

$$\begin{array}{l} \quad COOH \\ \quad | \\ \quad CH_2 \\ \quad | \\ NH_2CHCOOH \end{array}$$

Aspartic acid (amino succinic acid)

12.

$$\begin{array}{c} CO.NH_2 \\ | \\ CH_2 \\ | \\ NH_2CHCOOH \end{array}$$

Asparagine

13.

$$\begin{array}{c} COOH \\ | \\ CH_2 \\ | \\ CH_2 \\ | \\ NH_2CHCOOH \end{array}$$

Glutamic acid (α-amino glutaric acid)

14.

$$\begin{array}{c} CO.NH_2 \\ | \\ CH_2 \\ | \\ CH_2 \\ | \\ NH_2CHCOOH \end{array}$$

Glutamine

(d) Basic Amino Acids

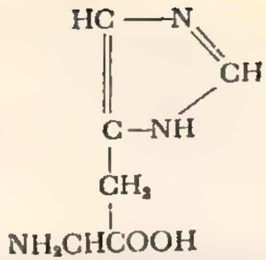
15.

$$\begin{array}{c} CH_2NH_2 \\ | \\ CH_2 \\ | \\ (CH_2)_2 \\ | \\ NH_2CHCOOH \end{array}$$

Lysine (diamino caproic acid)

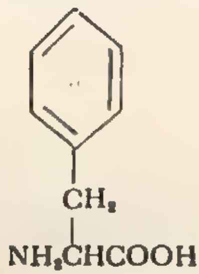
16.

$$\begin{array}{lll} CH_2 - NH - & C - NH_3 \\ | & \| \\ CH_2 & NH \\ | \\ CH_2 \\ | \\ NH_2CHCOOH \end{array}$$

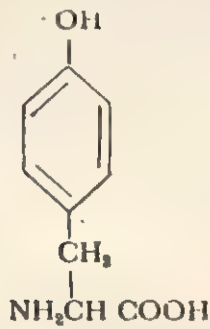
17. 

Histidine (α-amino, β-imidazolyl propionic acid)*

II. AROMATIC AMINO ACIDS

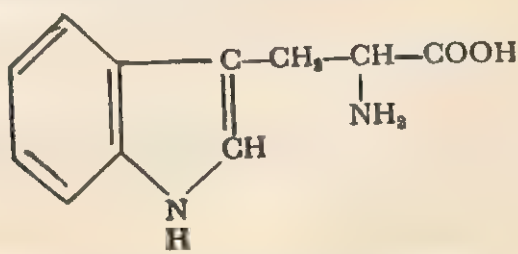
18. 

Phenylalanine (α-amino, β-phenyl propionic acid)

19. 

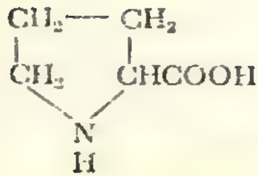
Tyrosine (α-amino, β-hydroxyl phenyl propionic acid)

III. HETEROCYCLIC AMINO ACIDS

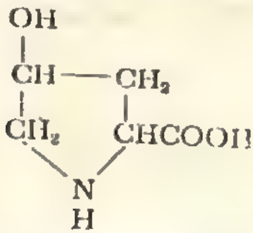
20. 

Tryptophan (α-amino, β-indole propionic acid)

*Also classified as heterocyclic amino acid.

21. 

Proline (Pyrrolidine-2-carboxylic acid)

22. 

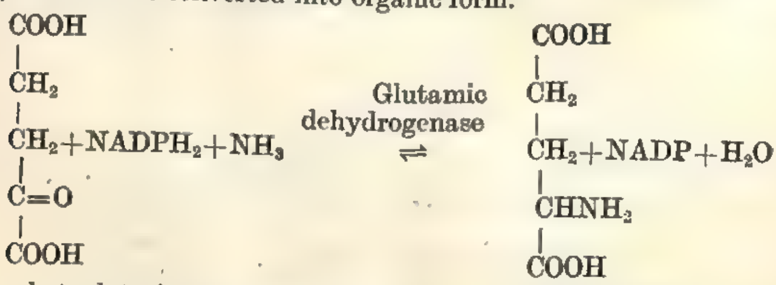
Hydroxy proline (4-hydroxy pyrrolidine-2-carboxylic acid)

BIOSYNTHESIS OF AMINO ACIDS

Amino acids are synthesized in plants in the following ways :—

1. REDUCTIVE AMINATION

Inorganic nitrogen in the form of **NH_3** (produced as a result of reduction of nitrates or biological nitrogen fixation or obtained from the soil) reacts with **α-keto glutaric acid** (an intermediate of Kreb's Cycle) in the presence of enzyme *glutamic dehydrogenase* and reduced coenzyme **$NADPH_2$** to form an amino acid, the **glutamic acid**, and thus is converted into organic form.



α-ketoglutaric acid glutamic acid

Because this process of conversion of the inorganic nitrogen (NH_3) into organic nitrogen (amino acid) is accompanied by **amination** and **reduction** at the **keto. group** of the organic acid hence, it is called as **reductive amination.**

2. TRANSAMINATION

The various other amino acids which ultimately condense to form proteins are produced by **Transamination** reactions involving

the transfer of **amino group** from glutamic acid to the **keto** position of the corresponding keto acid.

Amino group from other amino acids except glutamic acid may also be transferred to other kepto acids forming corresponding amino acids.

Transamination reactions take place in the presence of enzymes *Transaminases* which require coenzyme **pyridoxal phosphate** (a derivative of *vitamin B_6 i.e., pyridoxine*).

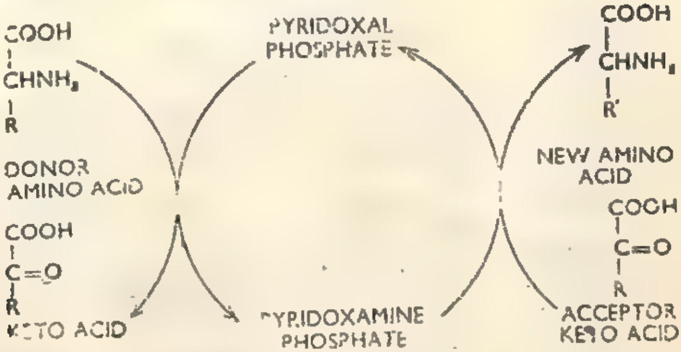
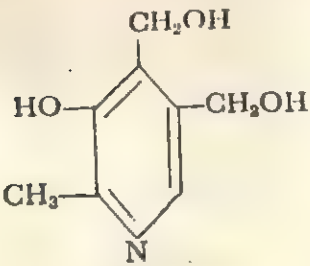
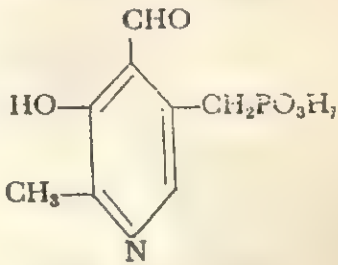


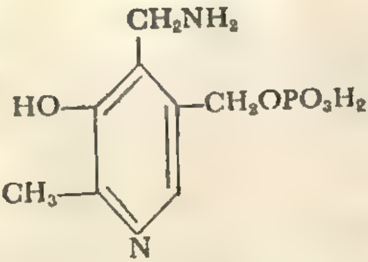
Fig. 22. Transamination



Pyridoxin



Pyridoxal phosphate

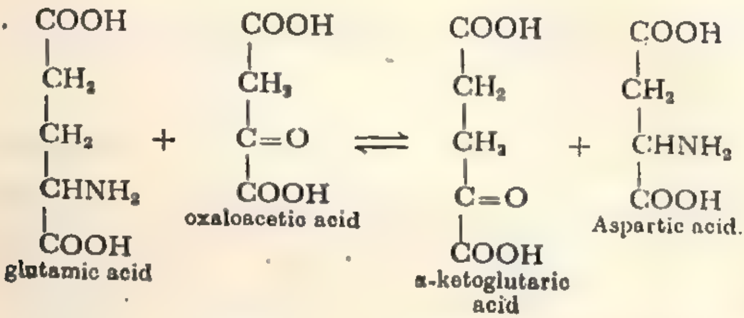


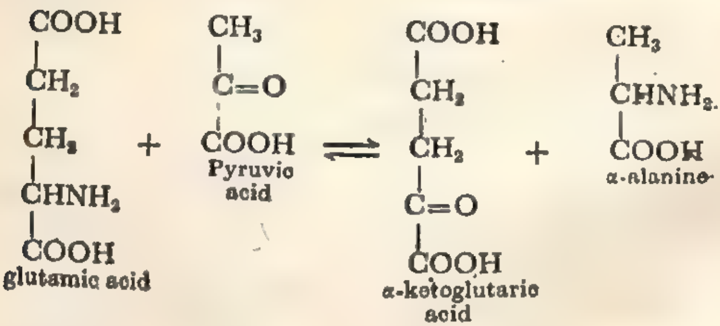
Pyridoxamine phosphate

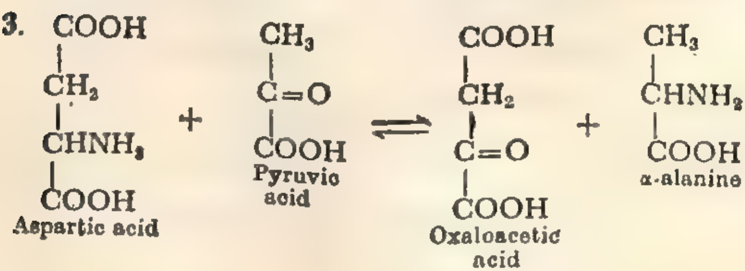
Fig. 23. Structures of Pyridoxin and its derivatives which act as coenzymes during transamination reactions.

The coenzyme pyridoxal phosphate acts as carrier of amino group. It picks up the amino group from the donor amino acid and is converted into **pyridoxamine phosphate**. The latter transfers this amino group to the acceptor keto acid forming a **new amino acid** and itself is converted into pyridoxal phosphate as shown in the figure 22.

Although a large number of transamination reactions are now known but the following 3 are very common :—

1.


2.


3.


3. OTHER METHODS

Amino acids may also be produced by the transformation of acid amides and other nitrogenous compounds, or by the hydrolysis of proteins by proteolytic enzymes.

AMPHOTERIC NATURE OF THE AMINO ACIDS

Amino acids are **amphoteric** in nature because they show **basic** as well as **acidic** properties due to the presence of ionizable **amino** and **carboxylic** groups.

ZWITTER-ION

In amphoteric compounds *e.g.*, amino acids there are two ionizable groups

$$-NH_2 \rightarrow -NH_3^+$$

$$-COOH \rightarrow -COO^-$$

If there is simultaneous ionization at both the groups there will be two opposite charges on the ion. Such an ion is called as a **Zwitter-ion** (Fig. 24).

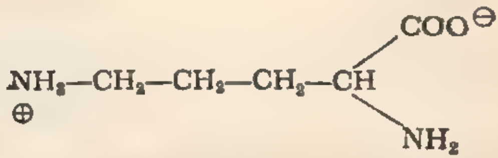


Fig. 24 . Zwitter-ion of ornithine

ISO-ELECTRIC POINT

As discussed earlier the amphoteric compounds like amino acids occur in Zwitter-ion state in solution, At lower pH (acidic) values there is excess of H^+ in the solution, the amino acids will be positively charged, since they will have excess $-NH_3^-$. On the other hand, at higher pH (alkaline) values the amino acids will be negatively charged due to excess $-COO^-$ groups, since the deficit of H^+ ions in the solution will be made up by the OH^- ions in the solution drawing H^+ ions from the $-COOH$ groups of the amino acids.

There will be a certain intermediate pH value where the number of positive and negative charges will be equal and the amino acids will become **neutral** or **uncharged**. This is called as the **isoelectric point.**

DISTRIBUTION OF THE NUCLEIC ACIDS

There are two types of nucleic acids *i.e.*, **DNA** (deoxy-ribose nucleic acid) and **RNA** (ribose nucleic acid).

(*i*) **DNA** which is the seat of all the hereditary characters is chiefly found in **chromatin** in the nucleus where it is associated with

proteins called as histones. Some DNA is also found in **Mitochondria** and **Chloroplasts**.

(*ii*) **RNAS** which are intimately associated with protein synthesis are found chiefly in **nucleolus** in the nucleus, **Ribosomes** and **Cytoplasm**. Besides this, RNA also occurs in **Mitochondria** and **Chloroplasts**. All plant viruses contain RNA.

CONSTITUENTS AND STRUCTURE OF NUCLEIC ACIDS

Nucleic acids are unbranched long-chain polymers of **nucleotides**. Each nucleotide consists of 3 parts :—

(*i*) a purine or pyrimidine base.

(*ii*) an aldopentose sugar.

(*iii*) orthophosphoric acid (H_3PO_4).

Different purine and pyrimidine bases found in the nucleic acids are :—

PURINES

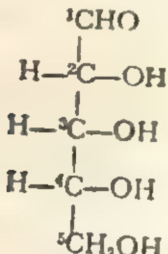
1. Adenine (A)
2. Guanine (G)

PYRIMIDINES

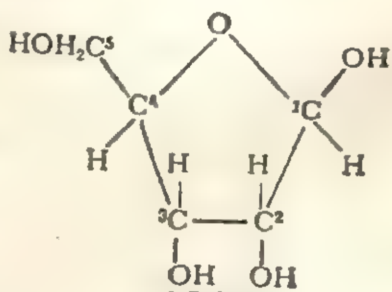
1. Thymine (T)
2. Cytosine (C)
3. Uracil (U)

The aldopentose sugar may be :—

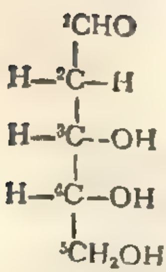
β-D-Ribose or β-D-2-deoxyribose.



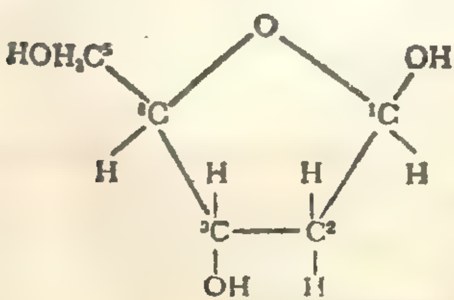
D-Ribose



β-D-Riboso



D-2-Deoxyribose



β-D-2-Deoxyribose

Combination of a base and pentose sugar is called as a **nucleoside.** If one of the C atoms (either 2, 3 or 5) of the pentose sugar in nucleoside is phosphorylated by $\mathbf{H_3PO_4}$, it is called as a **nucleotide** Fig. 25 (A).

Nucleic Acid

↓

Nucleotides

↙ ↘

Nucleoside + Orthophosphoric acid (H_3PO_4)

↙ ↘

Base + Aldopentose

Fig. 25 A. Diagrammatic representation of the constituents o. nucleic acid.

The nucleosides and nucleotides of the different bases are named as follows :—

Base	**Nucleoside**	**Nucleotide**
Adenine	Adenosine	Adenylic acid
Guanine	Guanosine	Guanylic acid
Thymine	Thymidine	Thymidylic acid
Cytosine	Cytidine	Cytidylic acid
Uracil	Uridine	Uridylic acid

The structure formulae of bases, nucleosides and nucleotides are given in Fig. 25 B, C and D respectively.

(**Note :** In DNA, the nucleosides and nucleotides of Adenine, Guanine, and Cytosine will contain β-D-2-deoxy ribose sugar.)

The nucleotides are joined together by **phosphorous ester links** between carbon no. 3 and 5 of the pentose sugars to form long **polynucleotide chains** that constitute the nucleic acids (Fig. 26).

That end of the polynucleotide chain at which the 3rd C atom of the sugar is free (not having phosphorous ester link) is called as **3'terminal end.** The other end with free 5th C-atom is called as **5'terminal end.**

Table 3. Difference between RNA & DNA

RNA	DNA
1. Single stranded structure.	1. Usually double stranded structure.
2. Bases are : Adenine, Guanine, Uracil and Cytosine.	2. Bases are : Adenine, Guanine, Thymine, and Cytosine.
3. Pentose Sugar is β-D Ribose,	3. Pentose sugar is β-D-2-deoxyribose (*i.e.*, O atom at 2nd carbon is absent).

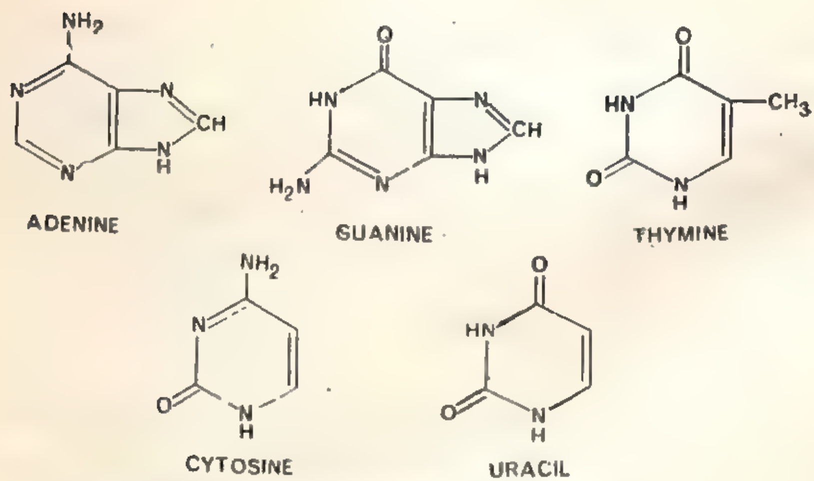


Fig. 25 B. Structures of purine and pyrimidine bases.

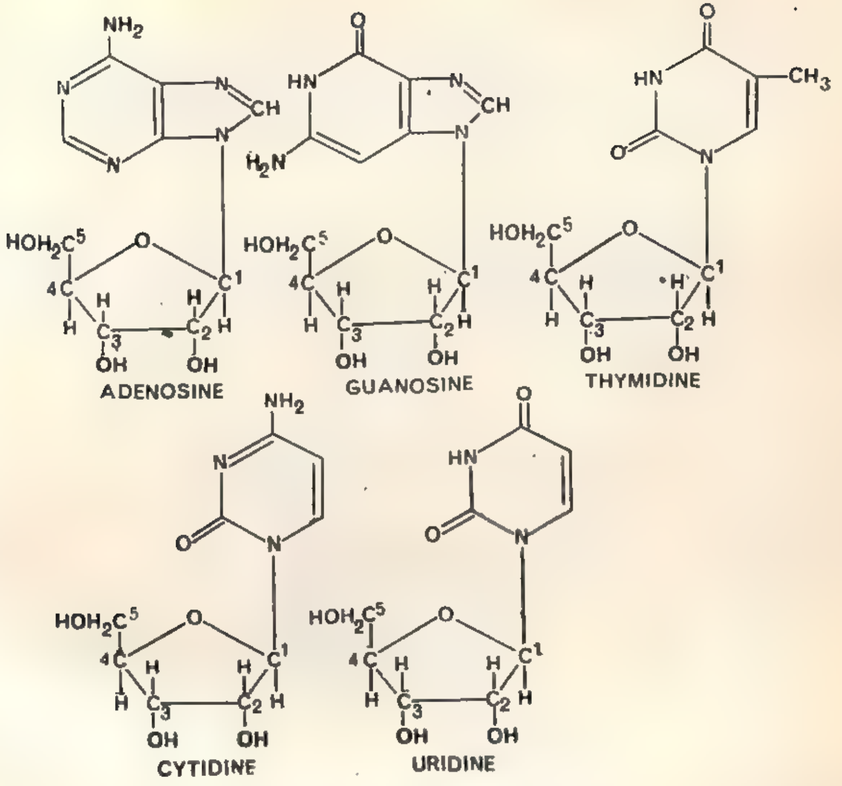


Fig. 25 C. Structures of nucleosides.

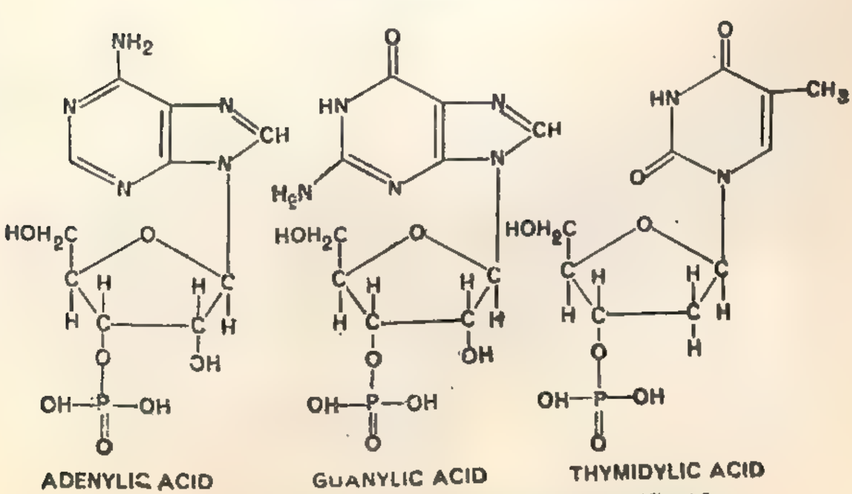
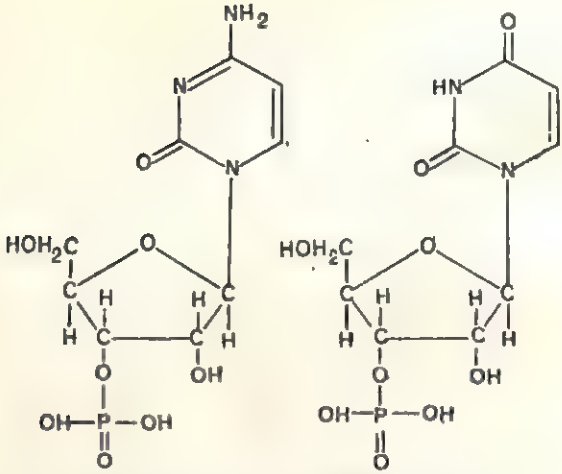
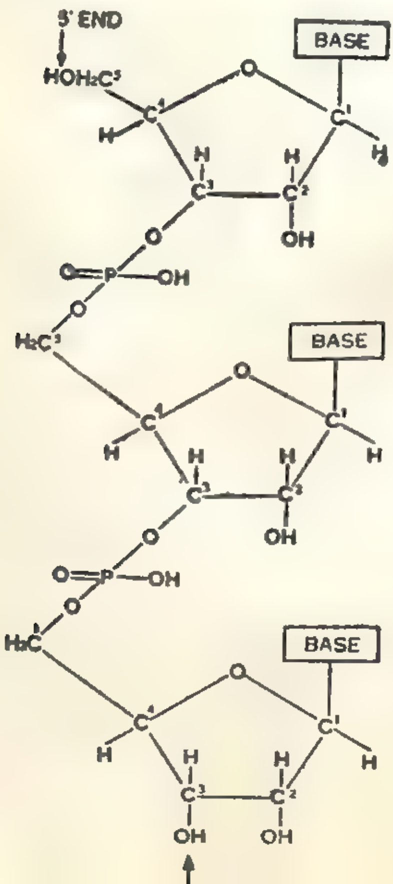


Fig. 25 D. Structures of nucleotides (Contd.)



CYTIDYLIC ACID URIDYLIC ACID

Fig. 25 D (Contd.), Structures of nucleotides.



DEOXYRIBOSE NUCLEIC ACID (DNA)

Watson and Crick (1953) have proposed a model for the structure of **DNA** molecule which is now usually accepted by all. According to this model called as **Waston-Crick Model**, the **DNA** molecule is a **double helix** structure consisting of **two long polynucleotide chains** coiled round each other around an **imaginary axis** and running opposite to each other. (Fig.27 A).

Each polynucleotide chain consists of thousands of necleotide units.

The back-bone of the two helices of polynucleotide chains consists of **deoxyribose phosphates** while the **bases** are present on the inner sides.

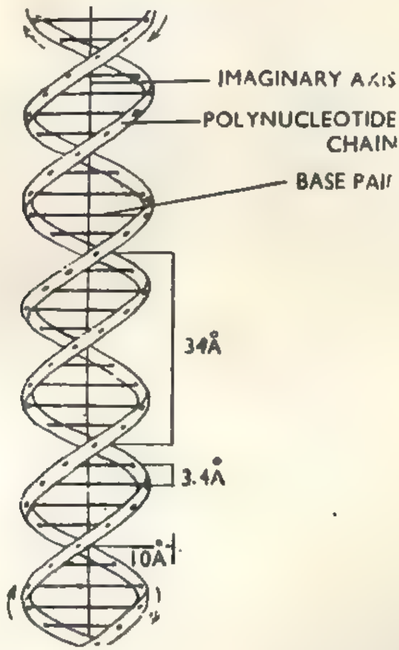


Fig. 27 A. The Watson-Crick model of DNA.

The bases of the one polynucleotide chain are **complementary** to the bases of the other polynucleotide chain and are joined together by **hydrogen bnods** (Fig. 27 C).

The **base pairing** is very specific (Fig. 27 B), The complementary bases are :—

Adenine and Thymine
Guanine and Cytosine

The ratio of purine and pyrimidine bases is 1 : 1.

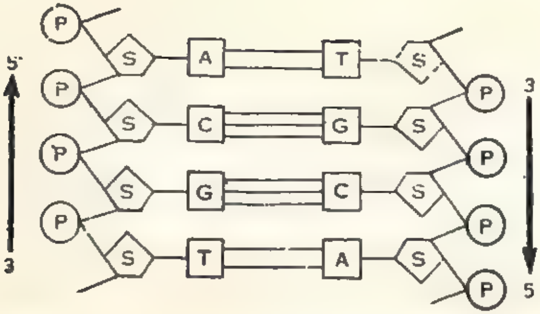


Fig. 27 B. Diagrammatic representation of a part of DNA molecule to show complementary base pairing.

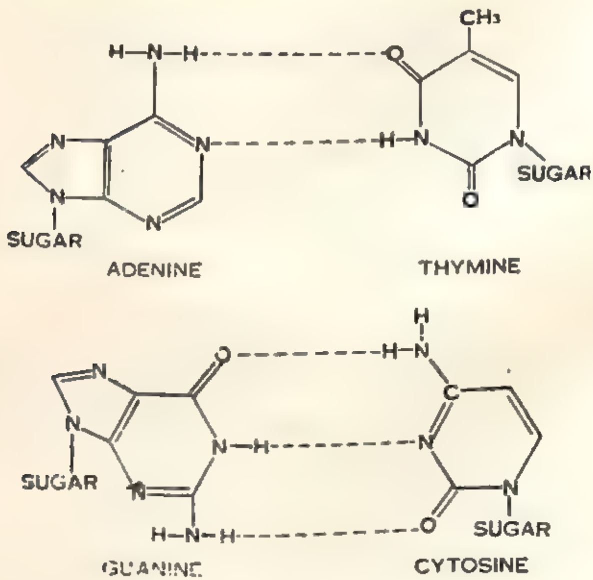


Fig. 27 C. Pairing of purine and pyrimidine bases by means of hydrogen bonding.

The distance between two subsequent bases in the polynucleotide chain is 3·4 Å.

Each turn of the two polynucleotide chain is completed after **10 bases** *i.e.*, a distance of 34 Å.

The distance between the axis and the sugar phosphate region is about 10 Å.

RIBOSE NUCLEIC ACID (RNA)

RNA is a **single stranded** structure consisting of only one polynucleotide chain. If sometime the complementary bases come very close to each other, hydrogen bonds are established between them to give polynucleotide chain a helical appearance like DNA.

RNA consists of the following bases :—

Adenine and Uracil

Guanine and Cytosine.

The ratio of purine and pyrimidine bases is not 1 : 1.

The pentose sugar is β-D-Ribose.

The size of RNA molecule is very small in comparison to the DNA molecule. Molecular wt. of RNA may range from several thousands to some lakhs.

There are 3 different forms of RNAs in plant cells :—

(1) Messenger RNA (m-RNA)

Molecular wt. of m-RNA is higher among different types of RNAs.

m-RNA is synthesized in nucleolus and after taking genetic information from **DNA** goes into the cytoplasm and helps in the formation of specific protein.

Sequence of 3 bases or nucleotides in **m-RNA** molecule constitutes a **Codon**. Actually the genetic information obtained from the DNA is encoded in codons which are specific (for details see genetic code).

(ii) Ribosomal RNA (r-RNA)

r-RNA is found in ribosomes which act as **template** for the synthesis of proteins.

(iii) Transfer or Soluble RNA (t-RNA or s-RNA)

The structures of many t-RNA molecules are known in quite detail. These are comparatively very small with a molecular weight of about 25000. Basic structure of all t-RNA molecules is on the **clover leaf** pattern. Clover leaf model of t-RNA is given in Fig. 28 A.

t-RNAs are found in cytoplasm and consist of only about 80 bases.

t-RNAs contain many unusual bases and nucleosides. These are *e.g.*, pseudouridine (ψ), dihydrouridine (DHU), inosine (I) etc. Methylation of bases is also common.

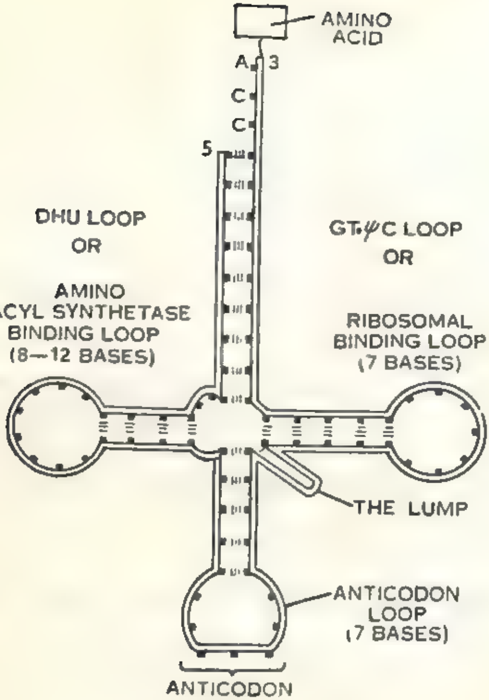


Fig. 28 A. Clover leaf model of t-RNA.

All t-RNA molecules contain Guanine (G) at 5′ end. The 3′ end always ends in the base sequence Cytosine-Cytosine-Adenine (CCA). During protein synthesis this end in fact picks up the amino acid and transfers it to the growing polypeptide chain and hence these RNAs are called as **t-RNAs or transfer RNAs**.

These t-RNAs are also called as **s-RNA or soluble RNAs** because they are soluble in **IM NaCl.**

t-RNA molecules are folded in a clover leaf pattern with three or more double helical regions (like DNA) terminating in loops. Three important loops of t-RNAs are (i) **anticodon loop** (ii) **amino acyl synthetase binding loop** and (iii) **ribosomal binding loop**.

Anticodon loop consists of 7 bases. At the free end 3 unpaired bases constitute the **anticodon** which is complementary to codon in m-RNA.

Aminoacyl synthetase binding loop consists of 8—12 bases. Because of the presence of dihydrouridines in this loop, it is also known as **DHU loop.**

The ribosomal binding loop consists of 7 bases. It contains sequence of GTψC and hence is also called as **GTψC loop**.

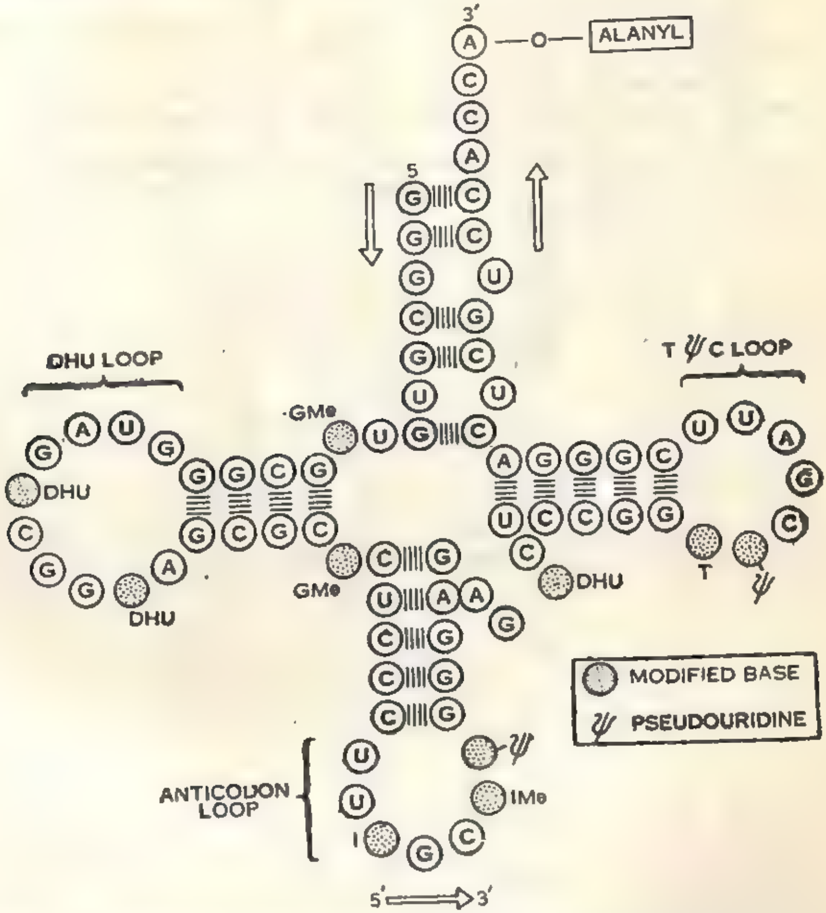


Fig. 28B. Detailed structure of Yeast alanyl-tRNA. (DHU = dihydrouridine, I = inosine. IMe = methyl inosine. GMe = methyl guanosine).

There are different t-RNA molecules with specific anticodons to pick up specific amino acids. However, many t-RNAs may be specific to a particular amino acid or a single t-RNA species may recognise several amino acids.

The t-RNA molecule whose structure was first given by **Holley** in detail is Yeast alanyl-tRNA (Fig. 28B).

REPLICATION OF DNA

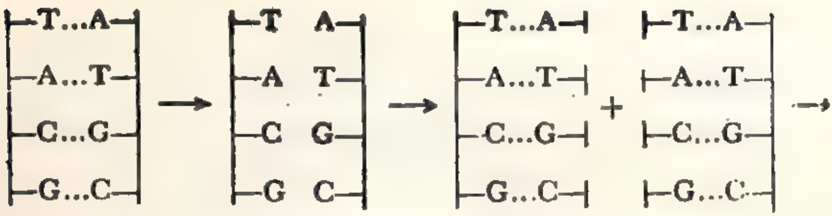
Formation of new **DNA** molecules from the parent **DNA** which are exactly similar to it (*i.e.*, its replica) is called as **replication of DNA.**

One of the very common methods of DNA replication which is called as **Semiconservative** method is as follows :—

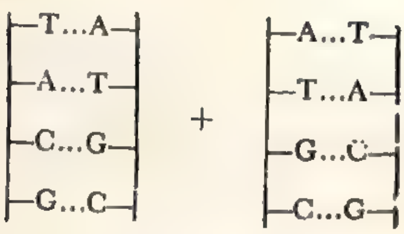
(*i*) The two polynucleotide chains of the parent DNA molecule separate due to breaking of H-bonds.

(*ii*) Free nucleotides are synthesized in the cell which are **complementary** to the nucleotides of the two separated chains.

(*iii*) The free nucleotides are joined together to form two new polynucleotide chains which are complementary to the two separated chains of parent DNA.



A DNA Molecule   Separated Polynucleotide Chains   Two Separated Polynucleotide Chains with Free Nucleotides aligned to them



Two DNA Molecules

Fig. 29·A. Semiconservative method of the replication of DNA molecule.

(*iv*) Each of the two new polynucleotide chains combines with complementary old polynucleotide chain by hydrogen bonds to form new DNA molecule (Fig. 29 A).

(*v*) Thus each of the two new DNA molecules consists of an old and a new polynucleotide chains.

It is thought that the polynucleotide chains begin to replicate themselves even before they are completely separated as shown in the Fig. 29 B.

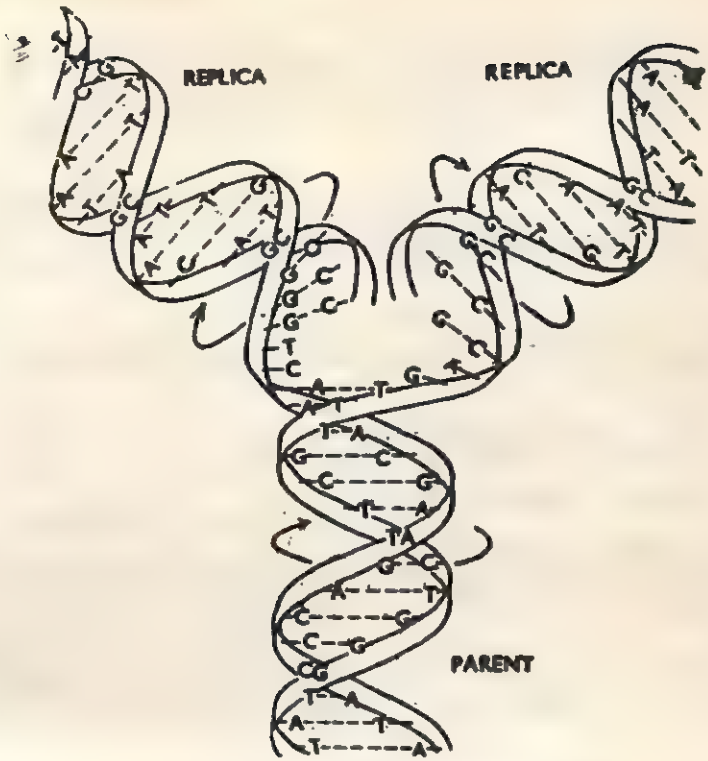


Fig. 29. B. Replication of DNA

GENETIC CODE

All the genetic information is encoded in **DNA** (in case of eukaryotes, in the DNA of nucleus) which produces hereditary characters in all the living beings.

In fact, this genetic information lies in the specific sequence of the nucleotides in polynucleotide chains of the **DNA.**

The first and the most important step in the manifestation of the genetic information (gene) is the formation of **specific protein** in which the sequence of amino acids is determined by the sequence of specific nucleotides of the polynucleotide chain of **DNA** molecule.

Various nucleotides that constitute the nucleic acids are represented by **code letters A,G,T,C,U.**

The sequence of 3 nucleotides in polynucleotide chains of the **DNA** molecule is called as **triplet code.**

In messenger RNA molecule (**m-RNA**) this sequence of 3 nucleotides is **Complementary** to the sequence of nucleotides in **DNA** and is called as **codon**. (A will be complementary to U and G to C and *vice versa*).

There are different codons for different amino acids. The latter are incorporated in a particular protein through specific **t-RNA** molecules with specific **anticodons**. Anticodon is complementary to codon.

Some of the codons like **UAA, UAG, UGA** can not select any amino acid and are called as **non-sense codons** or **Chain termination codons**.

A list of all the **codons** which specify amino acids constitutes the **coding dictionary** or **genetic code** (Table 4).

Some of the important features of the genetic code are :—

(i) It is **degenerate** *i.e.*, there may be more than one codons for a particular amino acid *e.g.*, **UUU, UUC**=phenyl alanine.

(ii) It is **non-overlapping** *i.e.*, only as many amino acids are coded as there are codons in end to end sequence *e.g.*, **UUUCCC** =phenylalanine (**UUU**)+proline (**CCC**).

(iii) It is **commaless** *i.e.*, there are no intermediary nucleotides (or commas) between the codons.

(iv) The first and the second letters of a codon are more important than the third in specifying an amino acid (Table 4).

SYNTHESIS OF PROTEINS IN PLANTS

Protein synthesis in plants is under the direct control of **DNA**. A brief account of the various steps involved in protein synthsis in plants is as follows :—

(i) **DNA** in the nucleus directs the synthesis of **m-RN/** and provides it with necessary genetic information in the form of **co..ns** for the formation of specific proteins. This process is called as **transcription**. **m-RNA** is synthesized in the presence of the enzyme RNA *polymerase*.

Table 4. Coding Dictionary or Genetic Code

FIRST LETTER	SECOND LETTER U		SECOND LETTER C		SECOND LETTER A		SECOND LETTER G		THIRD LETTER
U	UUU	Phe	UCU	Ser	UAU	Tyr	UGU	Cys	U
	UUC		UCC		UAC		UGC		C
	UUA	Leu	UCA		UAA**		UGA**		A
	UUG		UCG		UAG**		UGG	Tryp	G
C	CUU	Leu	CCU	Pro	CAU	His	CGU	Arg	U
	CUC		CCC		CAC		CGC		C
	CUA		CCA		CAA	GluN	CGA		A
	CUG		CCG		CAG		CGG		G
A	AUU	Ileu	ACU	Thr	AAU	AspN	AGU	Ser	U
	AUC		ACC		AAC		AGC		C
	AUA		ACA		AAA	Lys	AGA	Arg	A
	AUG	Met	ACG		AAG		AGG		G
G	GUU	Val	GCU	Ala	GAU	Asp	GGU	Gly	U
	GUC		GCC		GAC		GGC		C
	GUA		GCA		GAA	Glu	GGA		A
	GUG		GCG		GAG		GGG		G

**Chain termination codons or non-sense codons.

(Note : Names of amino acids against the codons are given in abbreviated form).

(*ii*) **m-RNA** molecule moves into the cytoplasm where it causes the formation of speific **t-RNA** molecules having specific **anticodons complementary** to its **codons**.

(*iii*) **m-RNA** becomes associated with the **ribosome** which acts as **template** for protein synthesis. At this template energy is supplied by **GTP** (Guanosine triphosphlate). Mg^{++} ions are also required.

(*iv*) **t-RNA** molecule picks up a specific amino acid by its **C-C-A end** (according to its anticodon) after the amino acid has been **activated** by **ATP** in the presence of a **specific enzyme** (Fig. 30).

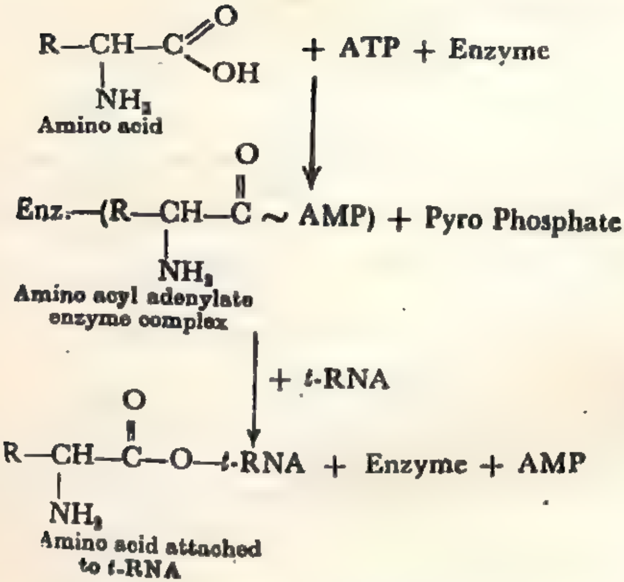


Fig. 30. Activation of the amino acid.

(v) In bacteria *Escherichia coli* the **70 S** ribosome dissociates into **30 S** and **50 S** subunits when **Mg^{++}** conc. is low. In higher plants the **80 S** ribosome breaks into **40 S** and **60 S** sub-units.

(vi) **30 S** subunit of the ribosme recognises the **5′ terminal end** of the m-RNA from where the protein synthesis *i.e.,* the formation of polypeptide chain starts.

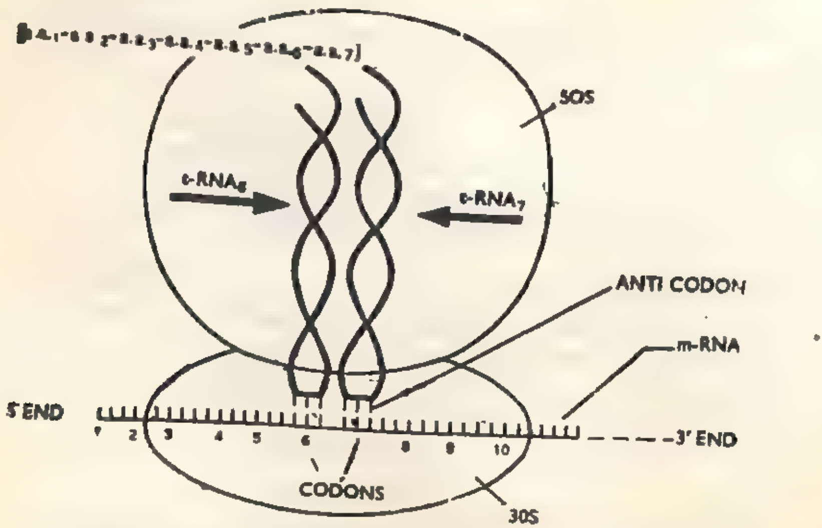


Fig. 31. The translation of the information carried by m-RNA into protein structure.

(*vii*) **30 S** subunit also recognises t-RNA—amino acid complex which is then transferred to **50 S** subunit. The first amino acid to be incorporated into the polypeptide chain is **N-Formlymethionie** for which the codons are **UUG, AUG** and **GUG**. Thus t-RNA—N-Formly-methionine-complex is the **initiator** of the polypeptide chain.

(*viii*) **30 S** and **50 S** subunits of the ribosome unite in the presence of **Mg⁺⁺** ions and become associated with **m-RNA**.

(*ix*) t-RNA-amino acid-complex attached to the ribosome is placed opposite the specific codon on **m-RNA** molecule due to the presence of its complementary **anticodon** in t-RNA molecule.

(*x*) Ribosome and the **m-RNA move** relative to each other. When ribosome reaches a second codon, another specific t-RNA-amino acid-complex is attached to the ribosome so that its anticodon is placed opposite its complementary codon (Fig. 31).

(*xi*) **A peptide bond** is established between the carboxylic and amino group of the two amino acids in the presence of the enzyme *peptide synthetase*. The preceding t-RNA-amino acid complex breaks so that **t-RNA** molecule is released into the cytoplasm to become charged again with amino acid.

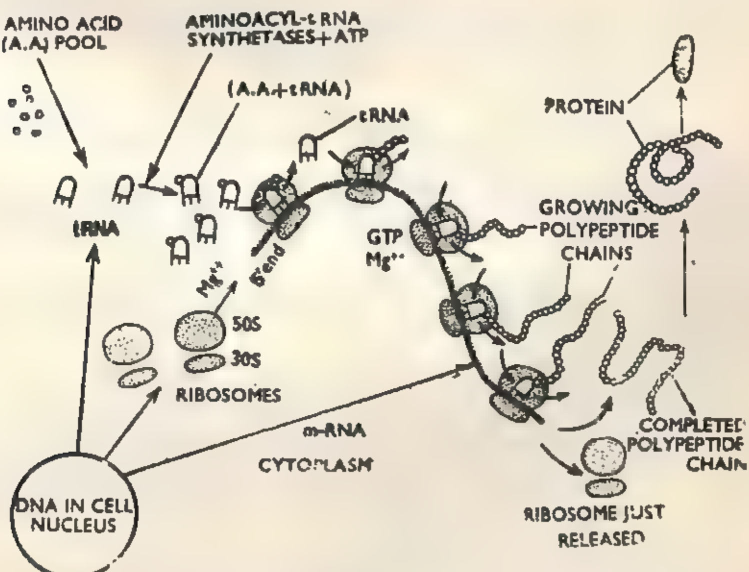


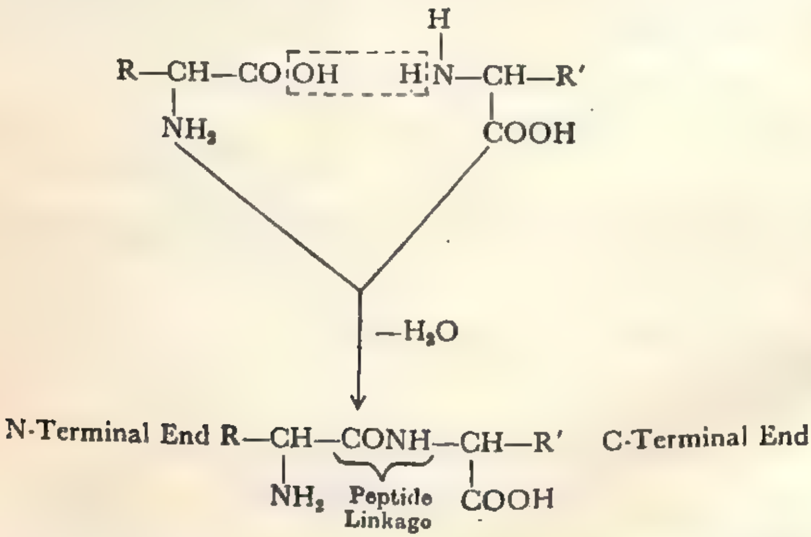
Fig. 32. A. Digrammatic representation of the complete process of protein synthesis.

(*xii*) In the same way, during the movement of the **m-RNA** and ribosome, a number of specific amino acids are added one after another into the **growing polypeptide chain**.

Peptide-linkage (**—CONH—**) is formed when **amino group** (**—NH_2**) of one amino acid condenses with **carboxylic group** (**—COOH**) of another amino acid eliminating one molecule of water.

That end of the polypeptide chain where the —COOH group of the amino acid is not involved in peptide linkage is called as **C-terminal end**. The other end of the polypeptide chain with amino acid having free—NH_2 group is called as **N-terminal end**.

Although there may be hundreds of amino acids in a single polypeptide chain but fundamentally there are only about 20 different



types of amino acids that constitute in proteins plants (there may be repetition of amino acids continuously or at intervals in the polypeptide (chain).

Because of their very large size the proteins are often called as **gigantic molecules** or **macromolecules** of the cells. Their molecular weight may range from few thousands to over a million (10 lakhs.)

STRUCTURE OF THE PROTEINS

The structure of the proteins can be studied under the following heads :—

(1) Primary Structure of the Proteins

Specific sequence or the arrangement of amino acids in the

polypeptide chain constitutes the primary structure of the proteins (Fig. 33).

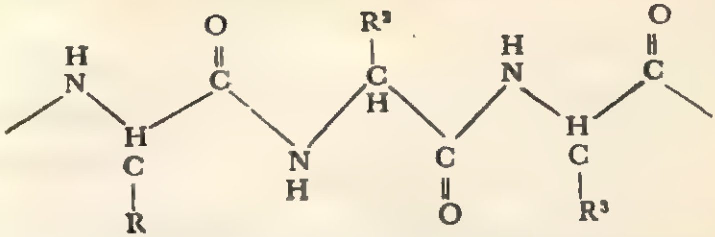


Fig. 33. Part of the polypeptide chain showing arrangement of amino acids.

(2) Secondary Structure of the Proteins (or α-Helix Structure)

Polypeptide chain of the protein molecule is held in a **coiled** or **helical** shape by **hydrogen bonds** which are established in between the peptide linkages. This coiled or helical shape of polypeptide chain constitutes the **α-helix** or **secondary structure** of the protein (Fig. 34).

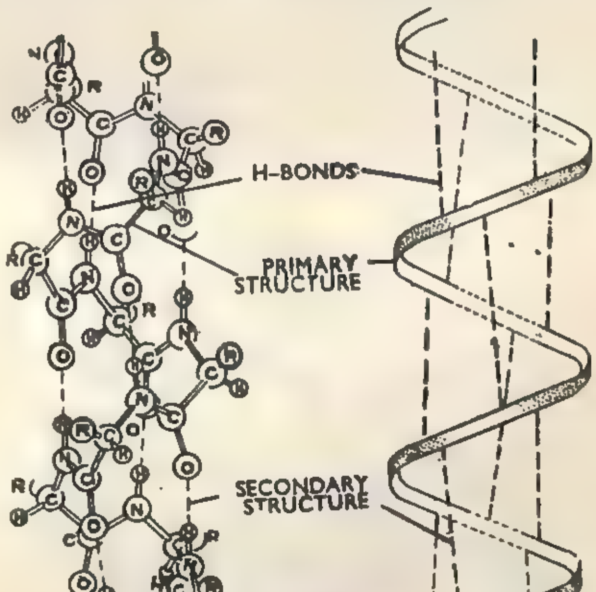


Fig. 34. α-helix structure of a protein
(A) Molecular (B) Diagrammatic

Although hydrogen bonds are very weak but when they are present in very large number all along the backbone of the polypeptide chain, they reinforce one another to stabilize the helical structure.

In a typical helical protein,

- each **NH** group (of peptide bond) is connected to a **C=O** group (of another peptide bond) by a **H**-bond at a distance equivalent to 3 amino acid residues.
- an α-helix or complete turn of a coil contains about 3.67 anino acid residues.
- the **pitch** of the helix is 5·4Å (vertical distance along the axis from any point on the helix to a corresponding point directly above it is called as the pitch of the helix).
- therefore, each amino acid is about 1·5Å (5·4/3·6) distant from the next amino acid residue.

(3) Tertiary Structure of the Proteins.

The coiled (α-helix) polypeptide chain is further **folded** in varoius ways. This folding which is very specific for a particular protein constitutes its **tertiary structure** and is determined by its primary structure (Fig. 35).

(Tertiary structure of the proteins is essential for biologically active proteins i.e., the enzymes. They are rendered useless (or are **denatured**) if their tertiary structure is lost).

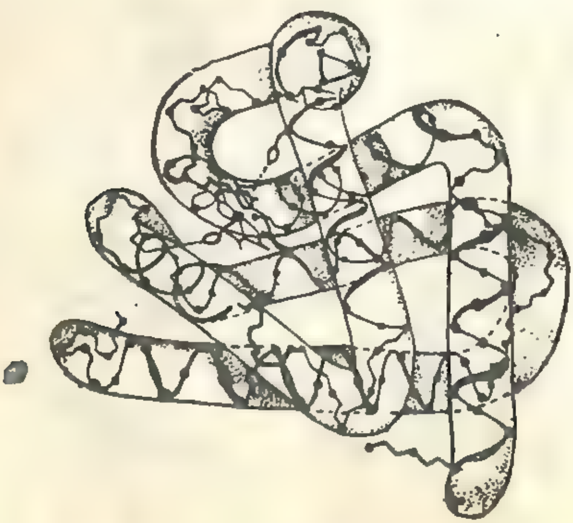


Fig. 35. Diagrammatic representation of the tertiary structure of a protein (sperm whale myoglobin).

The tertiary structure of the protein is stabilized by the following forces which have also been shown in fig. 36 .

- H-bonds (other than those established between the peptide linkages).
- Disulphide (S—S) bonds.
- Ionic-bonds or salt linkages.
- Steric Effects i.e., the interaction of non-polar side chains caused by the mutual repulsion of the solvent. .
- Van der Waals forces.

(All the molecules exert a weak force of attraction upon one another due to mutual interaction of their electrons and nuclei. There is a eletrostatic attraction between the electrons of one molecule and the nuclei of the other while on the other hand, there is electrostatic repulsion of nuclei and electrons of the molecule by the nuclei and electrons of the other molecule respectively. The resultant weak force of attraction between the two molecules is known as the Van der Waals attraction or Van der Waals force. The energy of such forces is about 1k. cal/mole.)

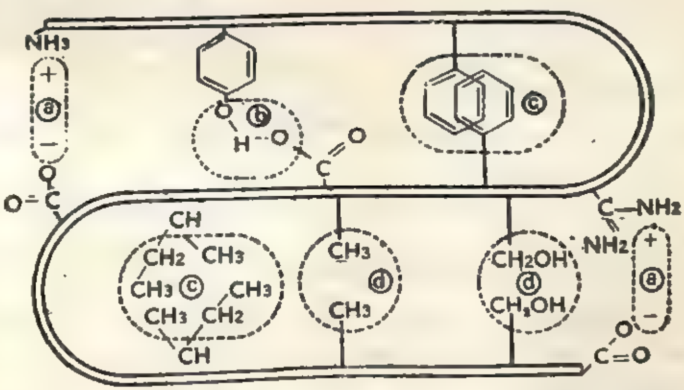


Fig. 36. Some types of non-covalent bonds which stabilize protein structure (a) electrostatic interaction (b) hydrogen bonding between tyrosine residues and carboxylate groups on side chains (c) interaction of non-polar side chains caused by the mutual repulsion of solvent (d) Vander Waals inter actions.

(4) Quaternary Structure of the Proteins

Sometimes more than one polypeptide chains are associated together to form a relatively more stable **super molecule** of protein. This constitutes the **quaternary structure** of the protein.

For example, in **blood hemoglobin** there are four polypeptide chains or sub-units that constitute the protein.

Quaternary structure is maintained by various forces like **disulphide-linkages, H-bonds** etc., between the different polypeptide chains of the protein.

CLASSIFICATION OF PROTEINS

On the basis of the nature of the products of hydrolysis by acids or proteolytic enzymes the proteins are grouped under two categories :—

(A) SIMPLE PROTEINS

These proteins on hydrolysis yield only amino acids. On the basis of solubility properties simple proteins are classified as follow :—

1. **Albumins.**

   Soluble in water and salt solutions.

2. **Globulins.**

   Sparingly soluble in water but soluble in salt solutions.

3. **Prolamins.**

   Soluble in 70—80% alcohol but insoluble in water and absolute alcohol.

4. **Glutelins.**

   Insoluble in all the above solvents but solube in acid or alkali.

5. **Scleroproteins.**

   Insoluble in aqueous solvents (found in animals only).

(B) CONJUGATE PROTEINS

These proteins on hydrolysis yield amino acids plus some non-amino acid part called as the **prosthetic group**.

Dependnig upon the nature of the prosthetic group associated with them, conjugate proteins are classified as follow :—

1. **Nucleoproteins (or Histones).**

   These are associated with nucleic acids.

2. **Glycoproteins.**

   These are associated with some carbohydrate.

4. **Chromoproteins.**

   These proteins are associated with some colouring matter *e.g.*, chlorophylls, carotenoids, phycobillins etc

4. Lipo-proteins.

These are associated with some lipid or fatty substances. (They are chiefly found in cytomembranes).

5. Iron-prophyrin Proteins.

These are associated with iron-prophylrin compounds *e.g.*, the cytochromes.

6. Simple Metal Containng Proteins.

These proteins are associated with some metal directly *e.g.*, **Ferredoxin** where **Fe** atoms are directly attached to the protein molecule.

7. Flavoproteins.

These are associated with some flavin compound *e.g.*, **FAD** (Flavin Adenine-Dinucleotide).

NITROGEN CYCLE

Ultimate source of nitrogen to all the living organisms is **molecular** or **atmospheric nitrogen** which constitutes about 80% of the air. This nitrogen after being **fixed** into **inorganic nitrogenous compounds** is consumed by the plants where it is converted into proteins etc., *i.e.*, **organic nitrogen** and is then eaten by the animals directly or indirectly. **Combustion** and **decay** of the dead plants and animals result in the release of free molecular nitrogen which goes into the air and the formation of simple inorganic compounds which are again taken up by the plants or are converted into free molecular nitrogen by **denitrification**.

Thus, the existence of the nitrogen cycle **maintains equilibrium of nitrogen in nature**. Some details of the various steps of the nitrogen cycle which is shown in Fig. 37 are as follow :—

(1) Some of the free molecular nitrogen of the atmosphere is fixed into nitrates **non-biologically** by lightening when oxygen of the air combines with nitrogen. The nitrogen so fixed is brought down into the soil along with the rains from where it is absorbed by the plants and is reduced to **ammonia**.

Atmospheric nitrogen is also fixed **biologically** by certain organisms like **legumes**, **some blue-green algae**, **some bacteria** etc., which convert it into **ammonia.**

Nitrates, Nitrites, and **ammonia** are also supplied to the soil artificially as **fertilizers**.

(2) Ammonia in plants is converted into organic form and is utilized in the synthesis of **proteins** and other organic nitrogenous compounds.

(3) Plant proteins are eaten by animals directly or indirectly through other smaller animals which they eat.

(4) Combustion of dead plant and animal bodies results in the production of free molecular nitrogen which again goes back into the atmosphere.

(5) Excreta of animals and dead organic nitrogenous matter produced as a result of the death of plants and animals are **decom-**

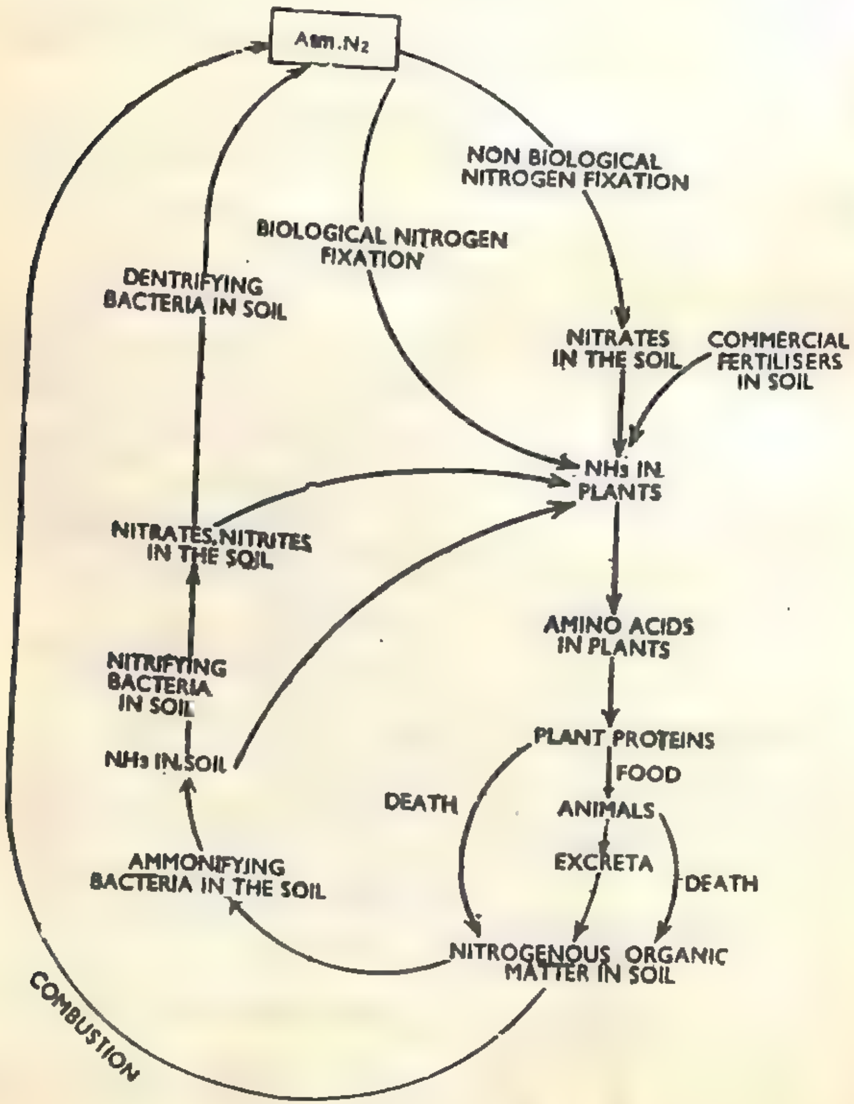


Fig. 37. Nitrogen cycle in nature

posed by certain **micro-organisms** in the soil through the processes of **ammonification** and **nitrification** to produce **ammonia, nitrates** and **nitrites** which may again be taken up by other plants.

(6) The nitrates and nitrites so produced may also be converted into **molecular nitrogen** by certain micro-organisms (denitrifying bacteria) *e.g., Bacillus denitrificans* present in the soil through a process called as **denitrification.**

Ammonification

Conversion of dead organic nitrogenous compounds in the soil **into ammonia** by **ammonifying bacteria** *e.g. Bacillvs mycoides, B. ramosus* and *B. valgaris* is called as **ammonification.**

Nitrification

Oxidation of ammonia produced by ammonification to **nitrates** by **nitrifying** bacteria is called as **nitrification.** It takes place in two steps :—

(*i*) In the first step the ammonia is oxidised to nitrites by nitrifying bacteria called as *Nitrosomonas* and *Nitrosococcus.*

$$2NH_3 + 3O_2 \rightarrow 2NHO_2 + 2H_2O$$

(*ii*) In the next step the nitrites are further oxidised to nitrates by another group of nitrifying bacteria called as *Nitrobacter.*

$$2HNO_3 + O_2 \rightarrow 2HNO_3$$

8

Enzymes

ENZYMES*

Most of the chemical reactions of the cells take place in the presence of **specific** proteinaceous substances called as the **enzymes.** They are functional at ordinary body temperature and are active usually within the cells (endoenzymes). Often, they are secreted by the cells and are active outside (exoenzymes). Enzymes may also be obtained in purified form from the cells without losing their catalytic activity and other properties.

The enzymes which are sometimes called as **biological catalysts** are essentially the **proteins** with a specific structure called as the **active centre** which may sometimes have an additional non-protein part, the **prosthetic group**.

The protein part of the enzyme is called as the **apoenzyme.** Complete enzyme including the prosthetic group is often called as **holoenzyme**.

Complete Enzyme
(holoenzyme)

Protein part **(apoenzyme)** + **Non-protein part** **(prosthetic group)**

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*The word *enzyme* is derived from *en + zyme* meaning in yeast. **Buchner** (1896) first showed that the yeast extract could bring about fermentation of grape juice and coined the word *zymase* for the active principle. It was **Sumner** who in 1926 solated the enzyme *Urease* in pure crystalline form which led to the establishment of protein nature of the enzymes. Since then large number of enzymes have been obtained in pure forms.

Some enzymes can be separated into many distinct forms each with essentially the same enzymatic activity which are called as **isozymes.** For example, the enzyme *lactate dehydrogenase* has been separated electrophoretically into 5 distinctly different forms, each with the same molecular weight (135,000) and with essentially the same enzymatic activity.

NOMENCLATURE OF THE ENZYMES

According to the older system the enzymes are usually named by adding suffix '**ase**' to the name of the substrate *e.g.*, *Maltase* from Maltose. *Lipases* from lipids. *Cellulase* from Cellulose etc.

Sometimes the name of the enzyme indicates the nature of the reaction *e.g., dehydrogenases.*

Sometimes enzyme name indicates the nature of the reaction and also the substrate *e.g., succinic dehydrogenase.*

The naming of the enzymes according to the older system has often been haphazard and sometimes confusing. For example, the enzyme names *pepsin, trypsin, papain* etc., do not give any indication of either the substrate or the reaction which they catalyse. Therefore, a systematic approach of naming (and also classifying) the enzymes has been recommended by the **Commission on Enzymes of the International Union of Biochemistry** (1961) according to which the various enzymes are designated by **code numbers** consisting of **four digits**. (For details see classification of enzymes).

CLASSIFICATION OF THE ENZYMES

(A) OLDER SYSTEM

According to the older system the enzymes are classified into two broad groups (*a*) **Hydrolysing enzymes** and (*b*) **Desmolysing enzymes.**

(a) HYDROLYSING ENZYMES

These enzymes hydrolyse and split the substrate molecule by the addition of water molecule. Some of the common hydrolysing enzymes are as follow :—

1. CARBOHYDRASES

Enzyme	Substrate	End—Products
(*i*) *Sucrase* (*Invertase*)	Sucrose	Glucose + Fructose
(*ii*) *Maltase*	Maltose	Glucose
(*iii*) *Amylase*	Starch	Maltose
(*iv*) *Cellobiase*	Cellobiose	Glucose
(*v*) *Lactase*	Lactose	Glucose + Galactose

(vi) *Cellulase*	Cellulose	Cellobiose.
(vii) *Inulase*	Inulin	Fructose

2. ESTERASES

(i) *Lipase*	Fat	Glycerol+fatty acids
(ii) *Phosphatase*	Phosphoric acid ester	Phosphoric acid +other compound

3. PHOSPHORYLASES

(i) *Sucrose-phosphorylase*	Sucrose+ Phosphoric acid	Fructose+ Glucose-1-Phosphate

4. PROTEOLYTIC ENZYMES

(i) *Pepsin*	Protein	Peptones
(ii) *Peptidases*	Polypeptides	Amino acids

5. AMIDASES

(i) *Urease*	Urea	NH_3+CO_2
(ii) *Asparaginase*	Asparagine	NH_3+Aspartic acid

(b) DESMOLYSING ENZYMES

These enzymes catalyse those reactions in which either the C-chain is broken or lengthened, or there is intramolecular or intermolecular transfer, addition or removal of atoms or chemical groups. Some examples of desmolysing enzymes are given below :—

1. DESMOLASES

(i) *Aldolase*	Fructose-1, 6-di phosphate	Dihydroxy acetone phosphate + 3-phospho-glyceraldeyde.

2. DEHYDROGENASES

(i) *Diphosphoglyceraldehyde dehydrogenase*	1, 3-Diphospho glyceraldehyde	1, 3-Diphospho-glyceric acid
(ii) *Alcohol dehydrogenase*	Alcohol	Acetaldehyde
(iii) *Lactic dehydrogenase*	Lactic acid	Pyruvic acid
(iv) *Succinic dehydrogenase*	Succinic acid	Fumaric acid
(v) *Malic dehydrogenase*	Malic acid	Oxalo-acetic acid

3. TRANSPHOSPHORYLASES

(*i*) *Phosphoglyceric transphosphorylase*	1, 3-Diphosphoglyceric acid + ADP	3-Phosphoglyceric acid + ATP
(*ii*) *Hexokinase*	Hexose sugar + ATP	Hexose phosphate + ADP

4. HYDRASES

(*i*) *Aconitase*	Aconitic acid + water mol.	Iso-citric acid
(*ii*) *Fumarase*	Fumaric acid + H_2O	Malic acid
(*iii*) *Enolase*	2-Phosphoglyceric acid	2-Phospho-Pyruvic acid + H_2O

5. TRANSAMINASES

(*i*) *Transaminases*	Aminoacid + keto acid	New Amino acid + Corresponding keto acid

6. CARBOXYLASES

(*i*) *Pyruvic acid Carboxylase*	Pyruvic acid	Acetaldehyde + CO_2

7. OXIDASES

(*i*) *Cytochrome Carboxylase*	Reduced Cytochrome	Oxidised Cytochrome

8. PEROXIDASES

(*i*) *Peroxidase*	Reduced compound + H_2O_2	Oxidised Compound + H_2O

9. CATALASES

(*i*) *Catalase*	H_2O_2	H_2O+Oxygen

(B) NEW SYSTEM

Main features of the new system of classification of the enzymes as recommended by the **Commission on Enzymes of the International Union of Biochemistry (1961)** are as follow :—

(*i*) All the known enzymes have been grouped in **6 major classes.**

(*ii*) Each major class has been divided into many **sub-classes.**

(*iii*) Each sub-class has been further sub-divided into **sub-sub-classes.**

(*iv*) Each enzyme has been assigned a specific **code number** consisting of **four digits**. The first digit indicates the major class, the second indicates the sub-class, the third digit indicates its sub-sub class while the fourth digit denotes the systematic **specific name of the enzyme** the **first part** of which indicates the name of the substrate and the **second part** the nature of the reaction.

MAJOR CLASSES

1. **Oxidoreductases**—Catalyse oxidation-reduction reactions.

2. **Transferases**—Catalyse reactions which involve group transfer.

3. **Hydrolases**—Catalyse hydrolytic reactions.

4. **Lyases**—Catalyse reactions in which either a double-bond is established due to the removal of a group, or a group is added to the double bond.

5. **Isomerases**—Catalyse isomerisation reactions.

6. **Ligases**—Also called as synthetases catalyse those reactions in which linking of two molecules is coupled with the breakdown of pyrophosphate bond of **ATP** or similar triphosphate.

Examples of some sub-classes, sub-sub classes, and specific enzymes are given below :

SUB-CLASSES

1·1. Oxidoreductase, acting on the **CH.OH** group of the donor.

2·1. Transferase, transferring one-carbon groups.

3·1. Hydrolase, which acts on ester links.

4·1. Lyase, acting on **C—C** bond.

5·1. Isomerase, which acts as racemase and epimerase.

6·1 Ligase, which forms **C—O** bonds.

SUB-SUB CLASSES

1·1·1. Oxidoreductase, acting on the **CH·OH** group of the donor, with coenzyme **NAD** or **NADP** as the acceptor.

2·1·1. Transferase, transferring one-carbon groups, and a methyl transferase.

3·1·1. Hydrolase, acting on carboxylic ester links.

4·1·1. Lyase, C—C lyase, carboxylase.

5·1·1. Isomerase, acting as a racemase and epimerase on amino acids and derivatives.

6·1·1. Ligase, which forms **C—O** bonds, amino acid—**RNA** ligase.

SPECIFIC ENZYMES

(With Trivial Names)

Code No.	Systematic Name	Trivial Name
1·1·1·1.	Alcohol : **NAD** Oxido reductase	Alcohol-dehydrogenase
2·1·1·1.	s-Adenosylmethionine : nicotinamide methyl transferase.	Nicotinamide methyl transferase
3·1·1·1.	Carboxylic ester hydrolase	Carboxylesterase
4·1·1·1.	2-oxi-acid carboxylyase	Pyruvate decarboxylase
5·1·1·1.	Alanine racemase	Alanine racemase
6·1·1·1.	L-Tyrosine : s-RNA ligase (AMP)	Tyrosyl-s-RNA Synthetase.

STRUCTURE OF ENZYMES

Structure of the enzymes can be studied in 3 parts :—

(1) Protein Part of the Enzymes (Apoenzyme)

Major portion of the enzyme cansists of protein whose molecular weight may vary from few thousands to over a million. For example,

Enzyme	Mol. Wt.
Ribonuclease	about 12700
Papain	about 20700
Glutamic dehydrogenase	over a million

Usually the enzymic proteins consist of only one polypeptide chain, but sometimes there may be more than one polypeptide chains.

Enzymic proteins consist of the same 20 different types of the amino acids which constitute other proteins.

Sequence of the amino acids is **specific** in specific enzymic proteins. Their tertiary structure is also very specific and important for their biological activity. Loss of the tertiary structure renders the enzyme inactive. For example, in enzyme *ribonuclease* different folds of the polypeptide chain are held together by **four disulphide linkages** (S—S) to give it a compact shape (Fig. 38 A). If these linkages are reduced with mercaptoethanol, the disulphide groups are converted to **sulphydryl groups** (—SH) resulting in unfolding of the polypeptide chain and loss of enzymic activity (Fig. 38 B). Reoxidation of the protein in air results in reformation of the disulphide bonds and return of its enzymic activity (Fig. 38 C).

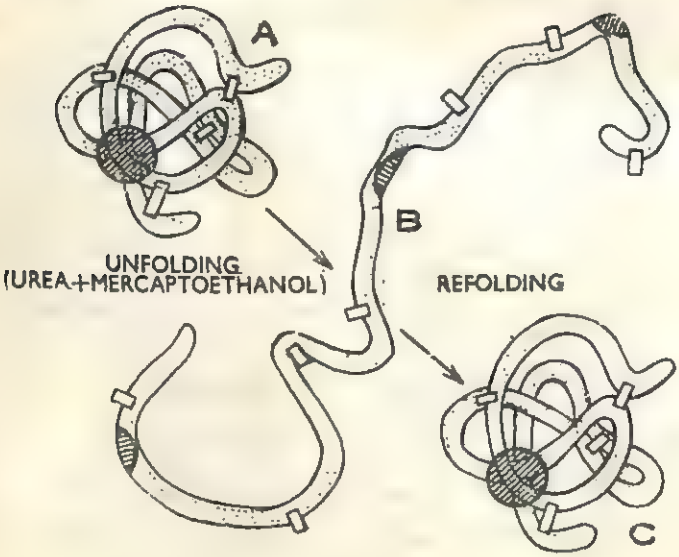


Fig. 38. A Native *ribonuclease* showing four disulphide bonds. Cross hatched area is the active site.
(B) Unfolded chain with broken disulphide bonds and active site.
(C) Refolding of chain and restoration of disulphide bonds.

(2) Active Centre (or Active Site)

Active centre or the active site is that part of the enzyme

which takes part in the reaction. Specific substrate combines with it and this combination brings about the biochemical reaction.

Active centre is very **specific**. There may be one or more active centres on a single enzyme molecule.

It is thought that the active centre consists of amino acid residues which are very close to each other in native structure of the enzyme because of the folding of the polypeptide chain, but in fact may be far apart in the primary sequence (Fig. 39). This also explains why unfolding of the polypeptide chain by denaturing agents results in loss of its activity.

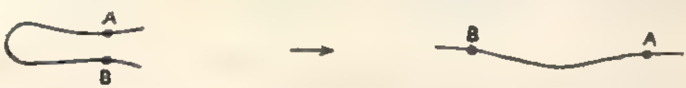


Fig. 39.

If the active centre is present only on one fold of the polypeptide chain and does not extend over the different folds as shown in Fig. 40, the unfolding of the poypeptide chain may not necessarily result in loss of enzyme activity.

Fig. 40

In enzymes consisting of more than one polypeptide chains, the active centre may extend on individual chain or over different polypeptide chains.

The neighbouring groups of amino acids although not constituting the active centre, may also have profound influence on its specificity.

(3) Prosthetic Group (non-protein part of the enzyme)

Sometimes a non-protein substance is required at the active centre for enzyme activity which is **bound tightly** to the enzyme protein by covalent linkages and is known as **prosthetic group**.

The prosthetic group may consist of (a) an organic compound or (b) simple metal ions such as Cu, Zn, Mn, Mo etc. The organic compounds acting as prosthetic groups are usually (*i*) a flavin compound such as **FMN** (Flavin Mono Nucleotide), **FAD** (Flavin Adenine Dinucleotide) (*ii*) heme-iron *i.e.*, iron-porphyrin or (*iii*) biotin etc.

COFACTORS

In many cases some non-protein chemical substances are required in the reaction mixture to catalyse the enzyme reaction. These substances which are **not tightly bound** to the enzyme are called as **cofactors**. Majority of the cofactors may be divided into 2 groups :—

(A) Specific Coenzymes

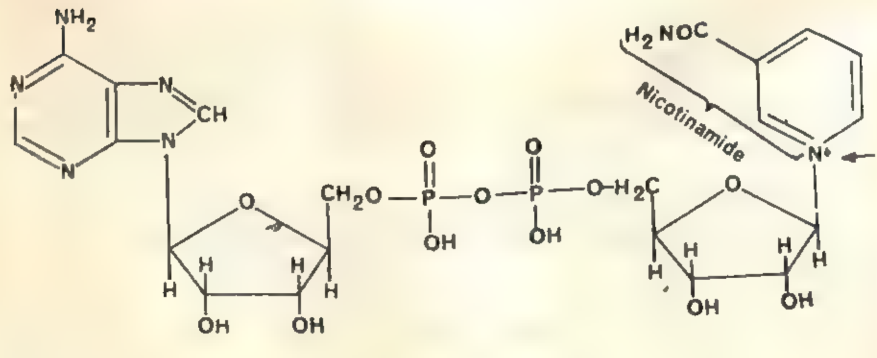
These are usually organic compounds of complicated structure often acting as carriers of some chemical group. Many coenzymes are either *vitamins* or derivatives of *vitamins*.

Depending upon the nature of the chemical group which they carry, the coenzymes are classified as follow :—

(1) Hydrogen Carriers (Oxidation-Reduction Reactions)

(i) **Coenzyme I** (CoI) or **NAD** (Nicotinamide Adenine Dinucleotide).

Previously known as **DPN** (Diphospho Pyridine Dinucleotide) it contains vitamin *Nicotinic acid* (*Niacin*) in amide form.

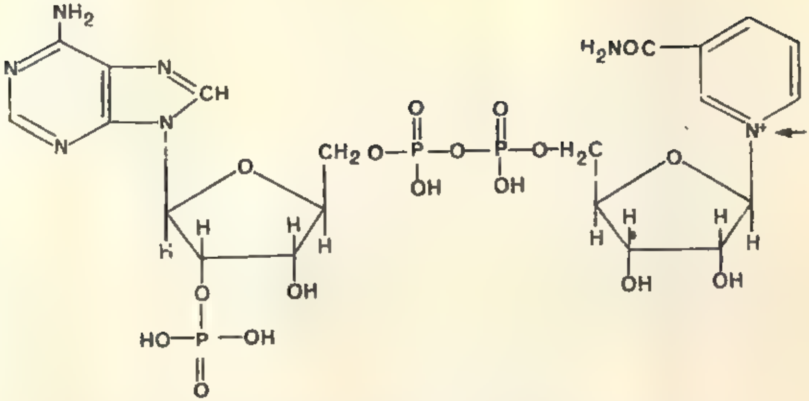


NAD$^+$ (DPN$^+$)—oxidised form.

(arrow indicates the position where reduction occurs)

(ii) **Coenzyme II** (Co II) or **NADP** (Nicotinamide Adenine Dinucleotide Phosphate).

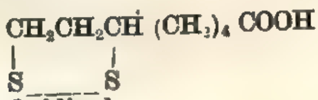
Previously known as **TPN** (Triphospho Pyridine Dinucleotide)



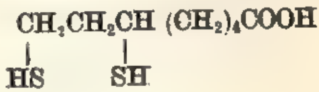
NADP$^+$ (**TPN**$^+$)— oxidised form.

(arrow indicates the position where reduction occurs)

(iii) Lipoic Acid (also helps in oxidative decarboxylation of α-keto acids).

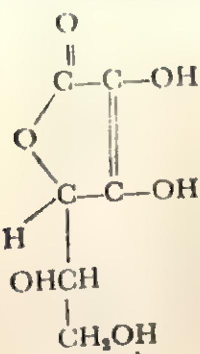


Oxidised

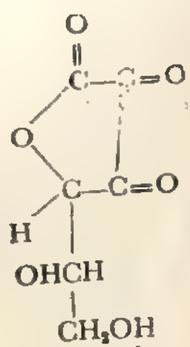


Reduced

(iv) Ascorbic Acid (*Vitamin* **C**)



Reduced



Oxidised

(v) **Glutathione**

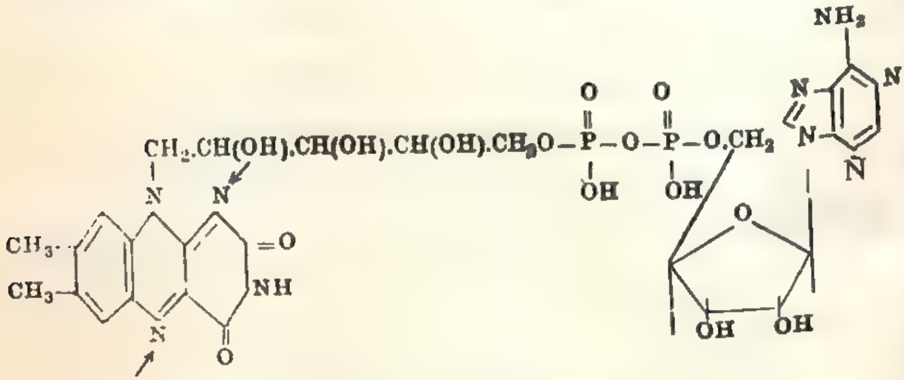
```
     CH2SH
       |
H—C—NH·CO·CH2·CH2.CH (NH2) COOH
       |
     CO NH·CH2COOH
```

Reduced form.

(arrow indicates the reactive group)

(vi) **Flavin Adenine Dinucleotide (FAD)**

It is derivative of *Vitamin* B_2 *i.e., Riboflavin.* Often it acts as prosthetic group.

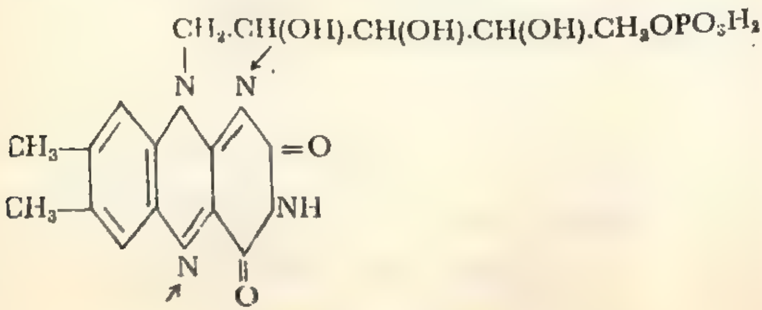


FAD (oxidised form)

(arrows indicate the positions where reduction takes place)

(vii) **Flavin Mono Nucleotide (FMN)**

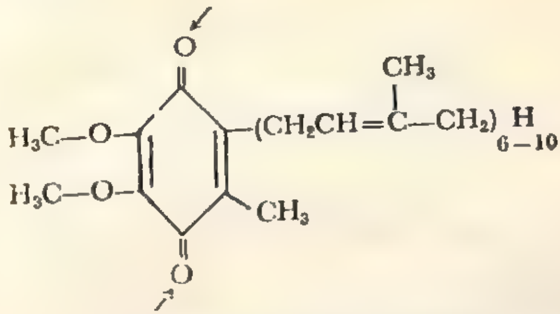
It is also derivative of *Vitamin* B_2 and often acts as prosthetic group.



FMN (oxidised form)

(arrows indicate the positions where reduction takes place)

(viii) Coenzyme Q (CO–Q) or Ubiquinone



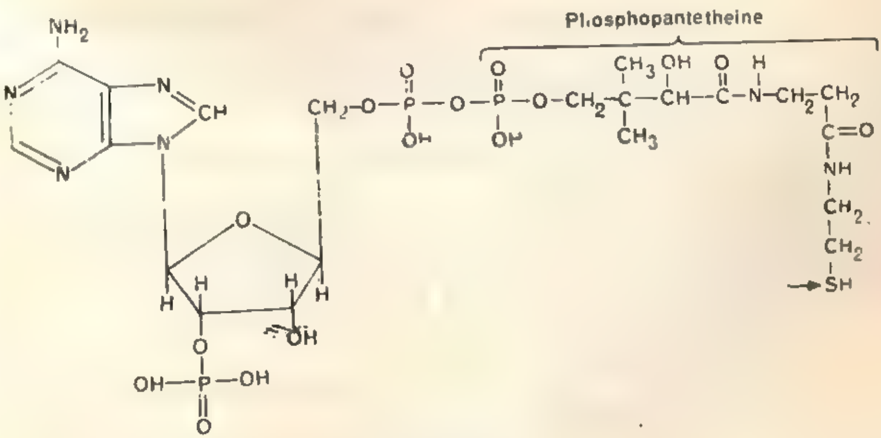
CO–Q (oxidised form)

(arrows indicate the positions where reduction occurs)

(2) Acyl Group Carrier

(i) Coenzyme A (CoA or CoA-SH)

It contains phosphopantetheine which is a derivative of the *vitamin pantothenic acid*.



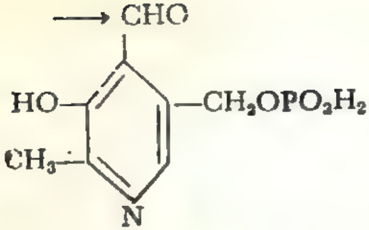
Coenzyme A

(arrow indicates the position where reduction occurs)

(3) Amino Group Carrier

(i) Pyridoxal Phosphate

It is drivative of *Vitamin B_6 i.e. Pyridoxin.*

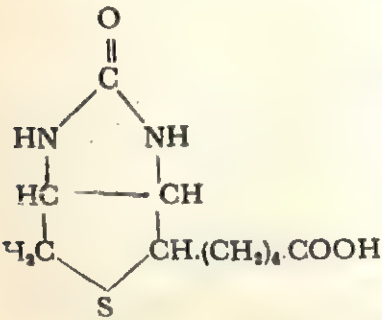


Pyridoxal phosphate
(arrow indicates the reactive group)

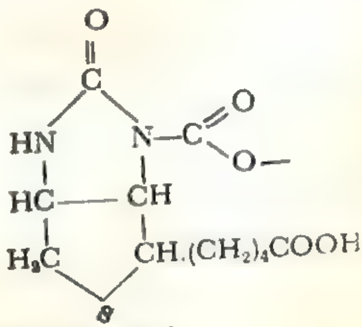
(4) CO_2 Carrier

(i) Biotin (Coenzyme R)

This is a *vitamin* and often acts as prosthetic group.



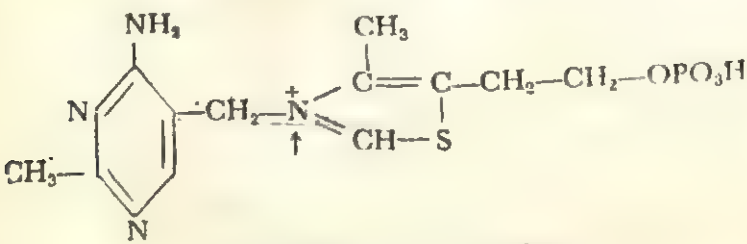
Biotin



Biotin-CO_2-Compound

(5) Thiamine Pyrophosphate (TPP) or Cocarboxylase

This is a derivative of *Vitamin B_1 i.e., Thiamine* and plays an important role as a coenzyme in the oxidative decarboxylation of α-keto acids (*e.g.*, pyruvic acid and α-ketoglutaric acid).

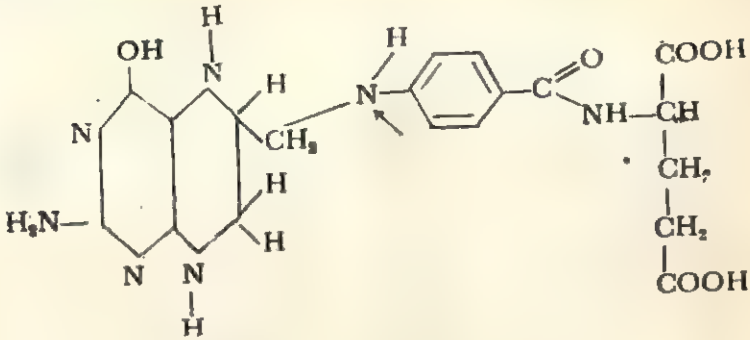


TPP (Thiamine Pyro Phosphate)
(arrow indicates the reactive part)

(6) Carrier of One-Carbon Compounds (*e.g.*, formic acid, formaldehyde).

(i) Coenzyme F (Tetrahydrofolic acid)

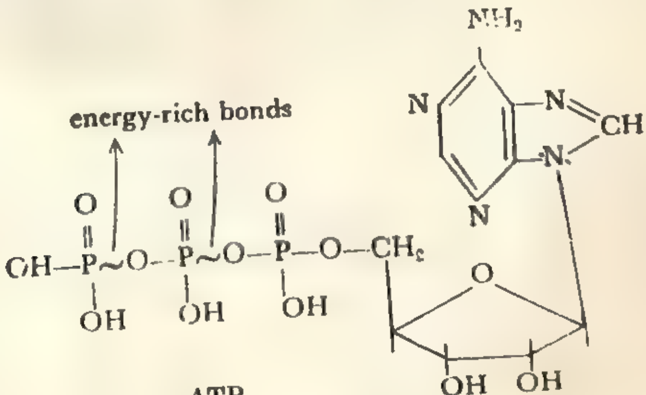
It is derivative of the *vitamin folic acid.*



Coenzyme F
(arrow indicates the functional part)

(7) Adenosine Tri Phosphate (ATP)

It acts as coenzyme and helps in catalysing many enzyme reactions by activating either the substrate or the enzyme and providing energy.



ATP

(B) General Activators

These are usually some metallic ions, the presence of which in someway activates the enzyme reaction.

MODE OF ACTION OF THE ENZYMES

According to **Fildes and Woods' Lock and Key** theory which is widely accepted there is physical contact between enzyme and

the substrate. As only a **specific key** fits in a particular **lock** to open it, similarly a **specific substrate** combines with the **active site** of the specific enzyme to form **Enzyme-Substrate Complex**. This enzyme-substrate complex breaks after the substrate has been converted into the **products** and the enzyme is again set free as shown in Fig. 41.

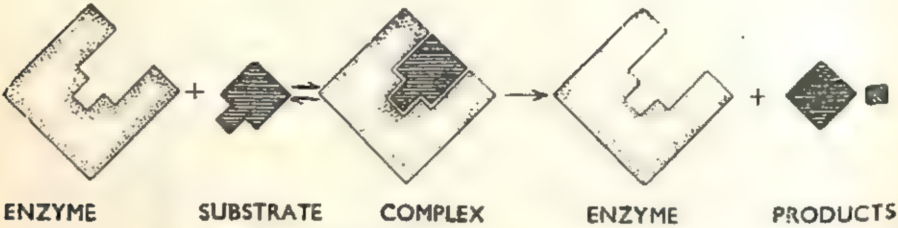


Fig. 41. Diagrammatic representation of an enzyme substrate reaction (Lock and Key Theory).

This theory is supported from the study of the **competitive inhibition** of the enzyme activity. Competitive inhibitors have some **structural similarity** with the substrate molecule both of which compete for the same active site on the enzyme. If even some part of the active site is preoccupied by competitive inhibitor, the substrate will not be able to combine with it and the activity of the enzyme is inhibited (a wrong key can not open a lock). Removal of the competitive inhibitor clears the way for substrate molecule to combine with the active site to form enzyme substrate complex so that enzyme activity is restored (For details see page 150).

However, there is yet another theory to explain the specificity of the enzymes which has been proposed by **Koshland** and is known as **Induced Fit Theory**. Recent experimental findings have proved this theory to be more compatible than the similar but older **Lock and Key Theory** which assigned a less flexible structure to the enzyme.

Koshland's Induced Fit Theory

According to this theory when a suitable substrate approaches the active site of the enzyme and as it forms the enzyme-substrate complex, the substrate **induces** some **conformational changes** in the enzyme. As a result, the attractive groups and buttressing groups form a complementary structure so that the catalytic group of the active site is in (or fits in) proximity of the bond (of the substrate) to be broken (Fig. 42 A).

After the suitable enzyme-substrate complex has been formed, the substrate molecule is held by hydrogen-bonds while a strain is

imposed on the bond of the substrate (which is to be broken) by the electrophilic and nucleophilic attack of the charged catalytic groups of the active site. The strain weakens the bond which is ultimately broken and the products are formed.

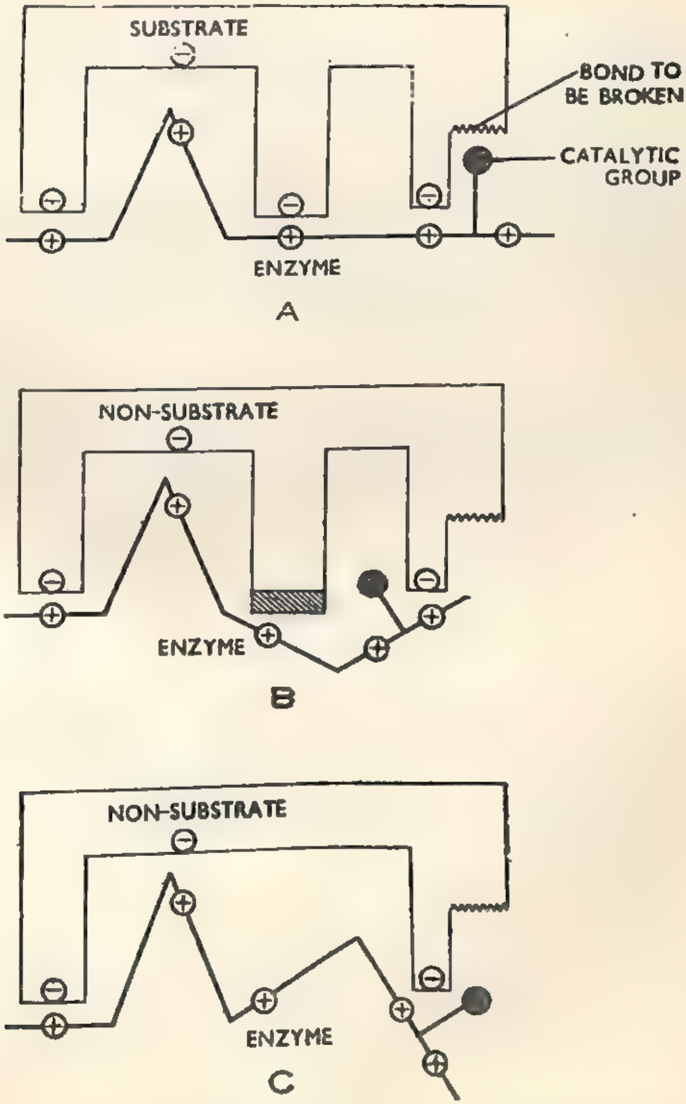


Fig. 42. Diagrammatic representation of Koshland's induced-fit theory. (see text).

In case, a non-substrate in which for example, an attractive

group is replaced by a larger group (Fig. 42 B) or which lacks one of the attractive groups (Fig. 42 C), approaches the active site of the enzyme a disorientation occurs so that the catalytic group is not in juxtaposition with the bond to be broken. And hence, reaction does not take place.

MECHANISM OF THE ENZYME ACTION

Arrhenius first pointed out that all the molecules in a given population do not have the same **kinetic energy**. Some molecules due to collisions have more energy and are **energy-rich molecules** while others are **energy-poor molecules**.

In an ordinary chemical reaction only energy-rich molecules can take part at normal temperature due to an **energy barrier** to reaction and hence, the rate of reaction is lower. The higher is the energy barrier for a molecule, the greater is its stability (or inactiveness to take part in reaction). The energy required to hurdle molecules over this energy barrier is called as the **energy of activation**.

At higher temperature the rate of chemical reaction becomes faster because increased temperatures bring about an increase in the number of **activated molecules** by increasing their movement and number of collisions due to **thermal agitation**.

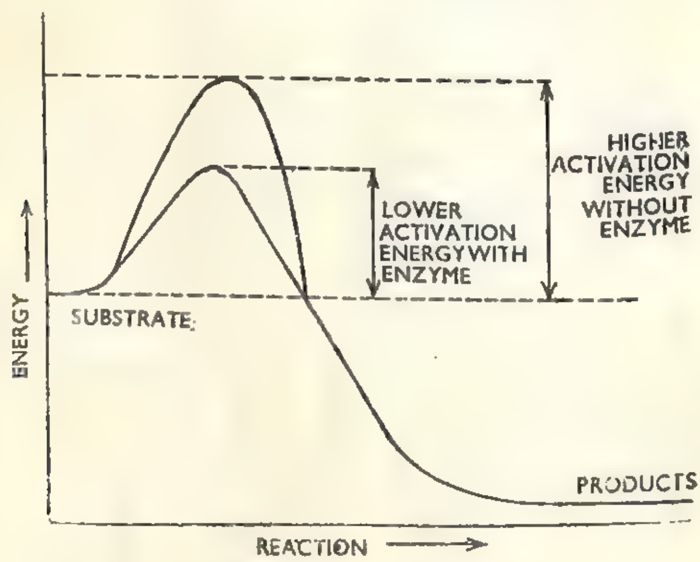


Fig. 43. Activation energy of an enzyme catalysed reaction is lower than that of an uncatalysed reaction.

But, in case is **enzyme catalysed reactions** the rate of reaction is **optimum** at normal body temperatures. It is because all the molecules (energy-rich and energy-poor) can combine with the active-sites of enzyme to form **enzyme substrate complex** which later on breaks into enzyme and the product. In other words, the enzymes act by **lowering the energy of activation of the reactions** (Fig. 43).

PROPERTIES OF ENZYMES

(1) Catalytic Property

Like inorganic catalysts the enzymes are active in very small or catalytic amounts and remain unchanged after the reaction. Only a small amount of enzyme is enough to convert large quantity of the substrate into products. Their **turnover number** *i.e.*, the number of substrate molecules converted by one molecule of the enzyme per second when its active site is saturated with the substrate, may range from 100 to over 3,000,000. The turnover number for *catalase* has been calculated as 10^6.

(2) Specificity

Enzymes are very specific in their action. A particular enzyme usually acts on a particular substrate to catalyse a particular type of reaction. In some cases the specificity of the enzymes may not be so strong but rather general and a particular enzyme may act on a group of substrates.

(3) Reversibility

In most of the cases the reactions catalysed by the enzymes are reversible depending upon the requirements of the cell. But, in some cases there are separate enzymes for forward and backward reactions. Or, a reaction catalysed by a particular enzyme may not be reversible at all.

(4) Sensitiveness to Heat and Inhibitors

(*i*) The enzymes are very sensitive to heat *i.e.*, they are **thermolabile**. They are inactivated at very low temperatures. At very high temperatures 60°–70°C usually they are destroyed (denatured). Low molecular weight enzymes are comparatively more heat stable.

(*ii*) Enzymes are also sensitive to inhibitors. While some inhibitors may partially inhibit their activity, other inhibitors like poisons destroy them permanently and inhibit their activity.

(5) Colloidal Nature

The enzymes are of colloidal dimensions and present large surfaces for reactants in water to facilitate the enzyme reaction.

FACTORS AFFECTING ENZYME ACTIVITY

(1) Temperature

Usually the activity of the enzymes is **optimum** at normal body temperature.

At very low temperature *i.e.*, about **0°C** the activity of the enzymes is **minimum**.

An increase in temperature up to a certain limit increases the enzyme activity, **maximum** being at about 45°C after which the enzyme activity is retarded (Fig. 44). Beyond 60° – 70°C usually their activity is permanently stopped due to the **denaturation** of enzymes.

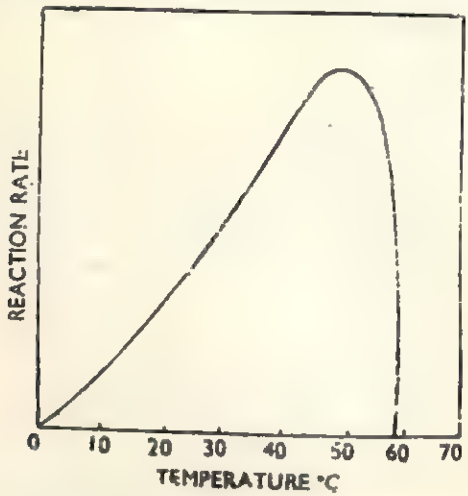


Fig. 44. Effect of temperature on enzymic reaction.

(2) Hydrogen Ion Concentration (pH)

Enzymes are active only over a limited range of pH. Some enzymes *e.g.*, *Trypsin* are active in alkaline medium (high pH), *Diastase* in neutral medium, while *Pepsin* shows optimum activity in acidic medium (low pH).

(3) Water

In absence of water the enzyme activity is suppressed so much so that in dry seeds the enzymes are almost inactive.

Proper hydration of the cells is necessary for enzyme activity because (*i*) water provides medium for enzyme reaction to take place, and (*ii*) in many cases it is one of the reactants.

(4) Concentration of the Substrate

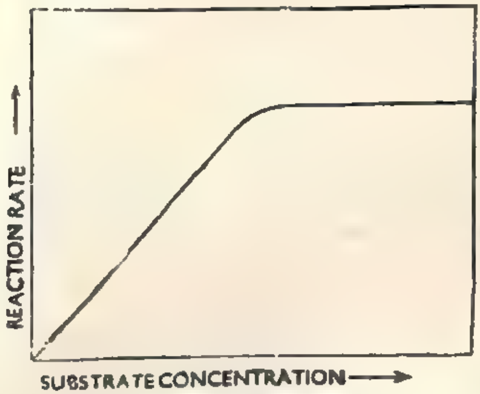


Fig. 45. Effect of substrate concentration on enzymic reaction.

Increase in the conc. of the substrate brings about an increase in the activity of the enzyme till all the **active sites** of the enzyme molecules are saturated with substrate. After this the rate of enzyme reaction becomes steady and addition of the substrate will not have positive effect (Fig. 45).

(5) Enzyme Concentration

Usually a very small amount of the enzyme can consume large amounts of the substrate. Increase in the conc. of the enzyme will increase the rate of reaction catalysed by it provided there is enough conc. of substrate (Fig. 46). It is because (*i*) the increased number of enzyme molecules will have more active sites, and (*ii*) at higher conc. of the enzyme the inhibitors will fall short.

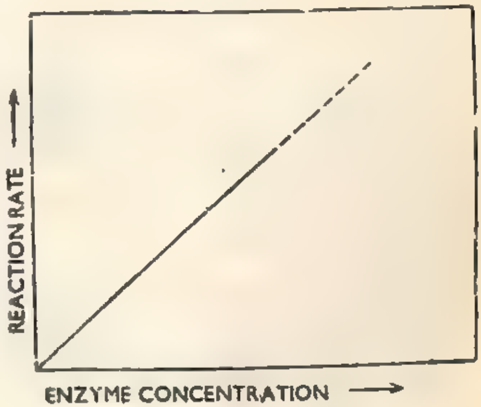


Fig. 46. Effect of enzyme concentration on the rate of reaction.

(6) Inhibitors

Presence of inhibitors in the reaction mixture inhibits the activity of the enzymes partially or completely depending upon the nature of the inhibitors. Inhibitors are less effective when the conc. of the enzyme and substrate is higher. Inhibitors are of two types :—

(i) Competitive Inhibitors

Such inhibitors have structural similarity with the substrate both of which **compete** for the same active site of the enzyme. If

competitive inhibitor pre-occupies the active site, the substrate molecule will be unable to combine with the enzyme and hence, the enzyme activity will be inhibited. But, this inhibition is of **reversible type** because removal of the competitive inhibitor restores the activity of the enzyme.

An example of competitive inhibitor is **malonic acid** which inhibits the activity of the enzyme *succinic dehydrogenase* which normally catalyses the conversion of succinic acid to fumaric acid. Inhibition of the activity of this enzyme is due to the structural similarity between malonic acid and succinic acid which has been shown diagrammatically in Fig. 47 .

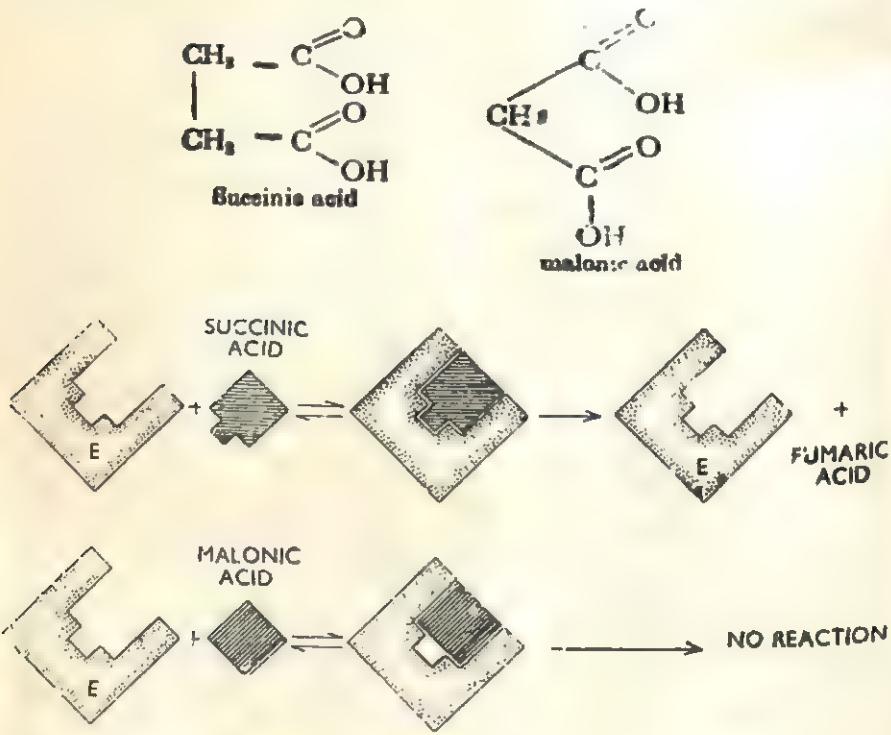


Fig. 47. Diagrammatic representation of the competitive inhibition.

(ii) Non-Competitive Inhibitors

These are usually **poisons** which do not compete for the active sites but destroy the structure of the enzyme and cause permanent or **irreversible-inhibition** of the activity of the enzyme.

(7) Accumulation of End-Products

Accumulation of the end-products retards the enzymic activity mainly because the active sites of the enzyme are crowded by them

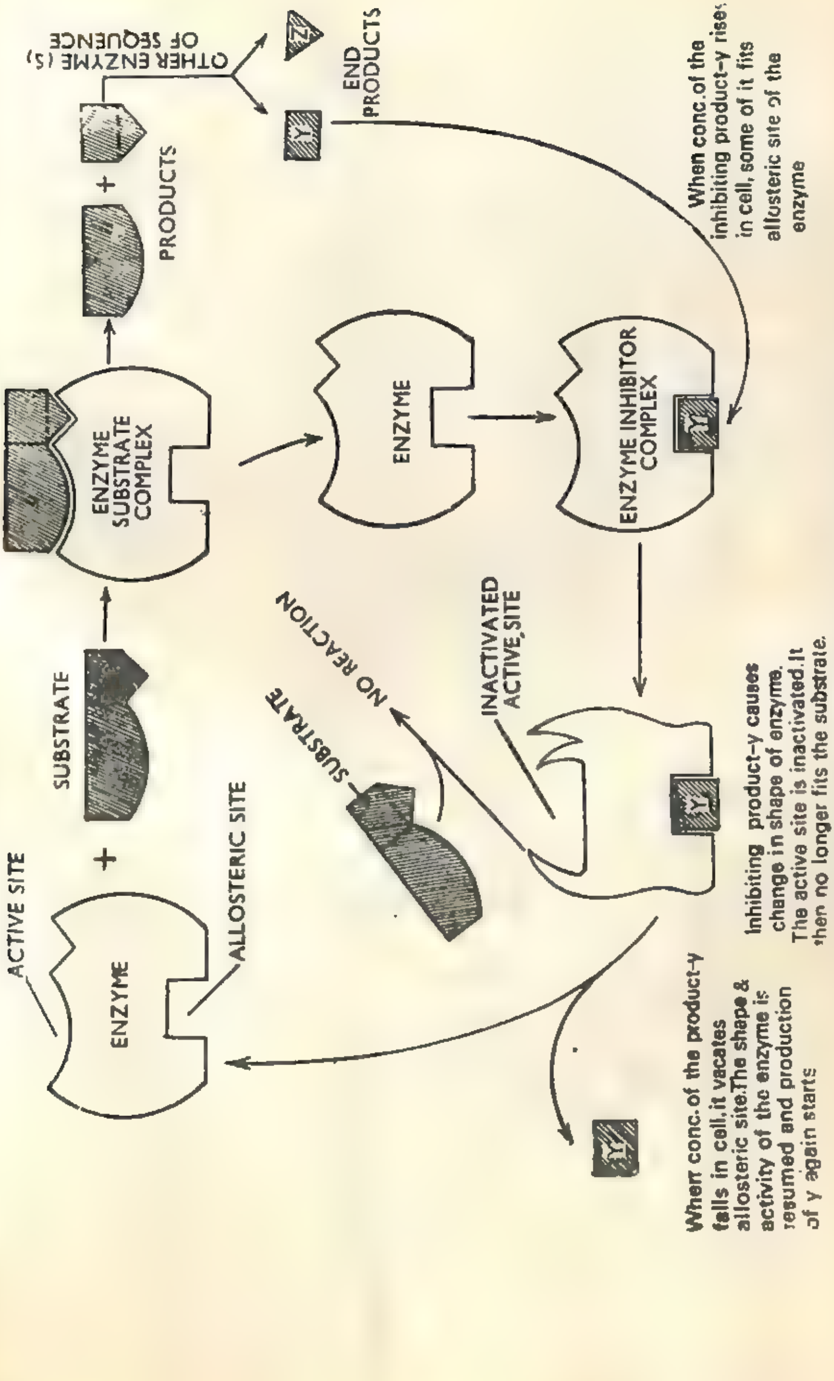


Fig. 48. **Diagrammatic representation of allosteric inhibition of an enzyme by a product of the reaction sequence.**

and the substrate molecules will have comparatively lesser chances of combining with the active sites.

ALLOSTERIC INHIBITION (OR FEEDBACK INHIBITION)

Sometimes it has been found that when a series of reactions is catalysed by a number of enzymes in sequence, the **accumulation of the final end-product** may cause inhibition in the activity of the **first enzyme** of the series. This inhibition due to a compound (final end product) which is totally different in structure from the substrate of the enzyme is called as **allosteric inhibition** or **feedback inhibition** and such an enzyme is called as **allosteric enzyme**.

This type of inhibition takes place due to the presence of **allosteric site** on the surface of the allosteric enzyme away from the active site. The final end-product molecule fits in the allosteric site and in some way brings about a **change in shaps** of the enzyme so that the active site of the enzyme becomes **unfit** for making complex with its substrate.

The allosteric inhibition is **reversible**. When the concentration of the final end product in the cell falls, it leaves the allosteric site, and the activity of the allosteric enzyme is restored.

Allosteric inhibition is shown diagrammatically in Fig. 48.

9

Photosynthesis

PHOTOSYNTHESIS

Although literary meaning of photosynthesis is 'synthesis with the help of light' but this term is usually applied to a very important vital process by which the green plants synthesize **organic matter** in presence of light. Photosynthesis is sometimes called as **carbon assimilation** and is represented by the following traditional equation.

$$6CO_2 + 6H_2O \xrightarrow[\text{Green Plant}]{\text{Light}} 6O_2 + C_6H_{12}O_6$$

During the process of photosynthesis the light energy is converted into **chemical energy** and is stored in the organic matter which is usually the carbohydrates and along with O_2 form the **end-products** of photosynthesis. One molecule of glucose ($C_6H_{12}O_6$) for instance, contains about **686 K. Cal.** of energy. **CO_2** and **H_2O** constitute the raw materials for this process.

About 90% of the total photosynthesis in the world is carried out by algae growing mainly in oceans* and also in fresh water.

Significance of Photosynthesis to Mankind

● It maintains equilibrium of O_2 in the atmosphere.

● It provides food either directly as vegetables, or indirectly as meat or milk of animals which in turn are fed on plants.

● Besides providing energy in the form of food, photosynthesis has also provided vast reserves of energy to man as **fuel** such as coal, oil, peat and also wood and dung.

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*This is an estimate by Rabinowatch (1951). According to more recent figures given by Ryther (1970) and Woodwell (1970), only one third of the total global photosynthesis can be attributed to the marine plants.

HISTORY OF PHOTOSYNTHESIS

The history of photosynthesis dates back to about 1648 when **Van Helmont** planted a 5 pounds willow shoot in 200 pounds of dried soil. After 5 years of watering with rain water the willow tree weighed 169 pounds. When the soil was dried and again reweighed, it was found to have lost only 2 ounces. He suggested that the increase in the plant substances of the willow tree must have come from water alone. Prior to this and from the time of **Aristotle** the idea was prevalent that the plants feed on **humus**

Stephan Hales (1727) pointed out that the plants obtained a part of their nutrition from the air and also suggested that sunlight may play a role in it.

Priestley (1772) showed that the plants might restore the air which has been "injured' (*i.e.*, laden with CO_2) by the burning of candles.

Ingenhousz (1779) noticed that only the green parts of the plants were able to purify the air and that too in the presence of sunlight.

Jean Senebier (1782) noted that the air-purifying activity of plants depends on the presence of fixed air (*i.e.*, CO_2) and suggested that the air (O_2) liberated by plants which are exposed to sunlight is the product of the transformation of fixed air (CO_2) by sunlight.

Nicolas Theodore de Saussure (1804) showed that the total weight of the organic matter produced and oxygen evolved by the green plants in presence of sunlight was greater than the weight of fixed air (CO_2) consumed by them during this process. He concluded that besides fixed air (CO_2), water must constitute the raw material for this process.

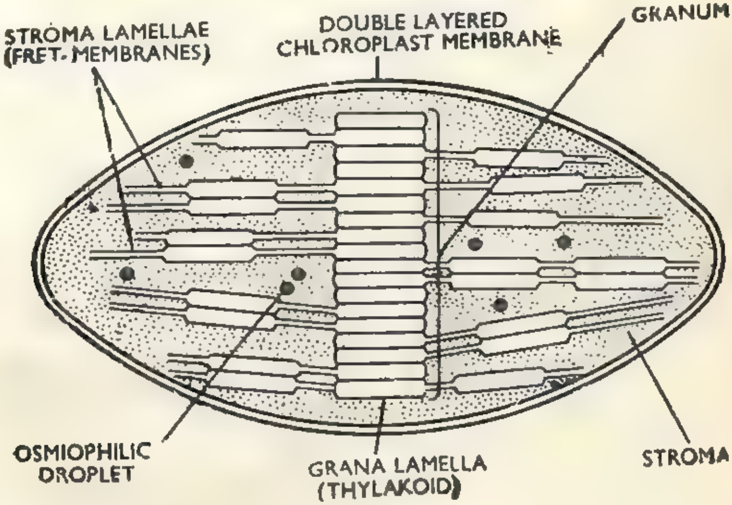
In 1845 **Meyer** recognised the role of light as a source of energy and thus it became possible to formulate the overall process of photosynthesis as conversion of water, CO_2 and light energy into O_2 and organic matter containing chemical energy by the green plants and which could be represented by the following equation.

$$CO_2 + H_2O \xrightarrow[\text{Green plants}]{\text{Light}} O_2 + \text{Organic Matter Containing Chemical Energy.}$$

In 1864 **Julius Sachs** showed that the process of photosynthesis takes place in **chloroplasts** and results in the synthesis of starch (organic matter).

PHOTOSYNTHETIC APPARATUS

The **chloroplasts** in green plants constitute the photosynthetic



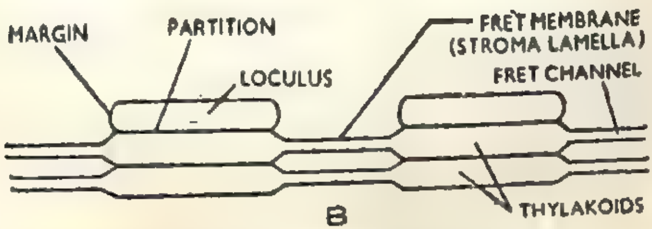


Fig. 49. A. Internal structure of a chloroplast.
B. Few enlarged thylakoids from two grana.

apparatus. Typically, the chloroplasts of higher plants are discoid or ellipsoidal in shape, 4-6 μ in length and 1-2 μ thick. The chloroplast is bounded by **two unit membranes** each app. 50 Å thick and consisting of **lipids** and **proteins**. The thickness of the two membranes including the space enclosed by them is app. 300 Å. Internally the chloroplast is filled with a hydrophilic matrix called as **stroma** in which are embedded **grana**. Each granum has a diameter of ·25—·8 μ and consists of 5-25 disk shaped **grana-lamellae** placed one above the other like the stack of coins (Fig. 49 A). In cross section these lamellae are paired to form sac like structures and have been called as **thylakoids**. Each grana lamella or thylakoid encloses a space, the **loculus**. The ends of disk-shaped thylakoids are called as **margins** (which are fused to form sac like structure) while the contiguous membranes between two thylakoids form the **partition** The grana lamellae or thylakoids consist of alternating layers of **lipids** and **proteins**

Some of the grana-lamellae or thylakoids of a granum are connected with thylakoids of other grana by somewhat thinner **stroma-lamellae** or **fret membranes**. These also enclose spaces which are called as **fret-channels** (Fig. 49 B).

Chlorophylls and other photosynthetic pigments are confined to grana. The latter are the sites of **primary photochemical reaction**. **Weier and Benson** (1966, 1967) have also included chlorophyll molecules in the fret membranes in their model of the ch'oroplasts.

Besides necessary enzymes, some ribosomes and DNA have also been found in chloroplasts which give them (chloroplasts) a **partial genetic autonomy**.

PHOTOSYNTHETIC PIGMENTS

Photosynthetic pigments are of three types :—

(1) **Chlorophylls**, (2) **Carotenoids**, and (3) **Phycobillins**.

- Chlorophylls and carotenoids are insoluble in water and can be extracted only with organic solvents.
- Phycobillins are soluble in water.
- Carotenoids include **carotenes** and **xanthophylls**. The latter are also called as **carotenols**.
- Different pigments absorb light of different wavelengths and show characteristic absorption peaks *in vivo* and *in vi'ro*.
- They show property of fluorescence.

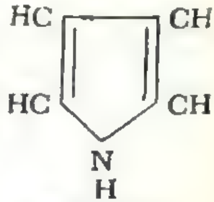
Distribution of Photosynthetic Pigments in Plant Kingdom.

The distribution of the different types of photosynthetic pigments in plant kingdom is shown in table 5.

Table 5. Distribution of Photosynthetic Pigments in Plant Kingdom.

Pigment	Distribution in Plant Kingdom
(1) **Chlorophylls** Chlorophyll a	All photosynthesizing plants except bacteria
Chlorophyll b	Higher plants and green algae
Chlorophyll c	Diatoms and brown algae
Chlorophyll d	In some red algae
Chlorophyll e	In *Tribonema* and zoospores of *Vaucheria*
Bacteriochlorophyll a	Purple and geen bacteria
Bacteriochlorophyll b	In a strain of purple bacterium *Rhodopseudomonas*
Chlorobium chlorophyll (Bacterioviridin)	Green bacteria
(2) **Carotenoids** Carotenes	Mostly in algae and higher plants
Xanthophylls (Carotenols)	Mostly in algae and higher plants
(3) **Phycobillins** Phycoerythrins	In blue-green and red algae
Phycocyanins	,,
Allophycocyanin	,,

Structure of Photosynthetic Pigments



Pyrrol ring

(1) **Chlorophylls**. They are **magnesium porphyrin** compounds. The porphyrin ring consists of four **pyrrol** rings joined together by **CH** bridges. A long chain of C atoms called as **phytol** chain is attached to porphyrin ring.

- Chemical structures of chlorophyll a and chlorophyll b are well established.

- Molecular formulae of chlorophyll a and chlorophyll b are $C_{55}H_{72}O_5N_4Mg$ and $C_{55}H_{70}O_6N_4Mg$ respectively.

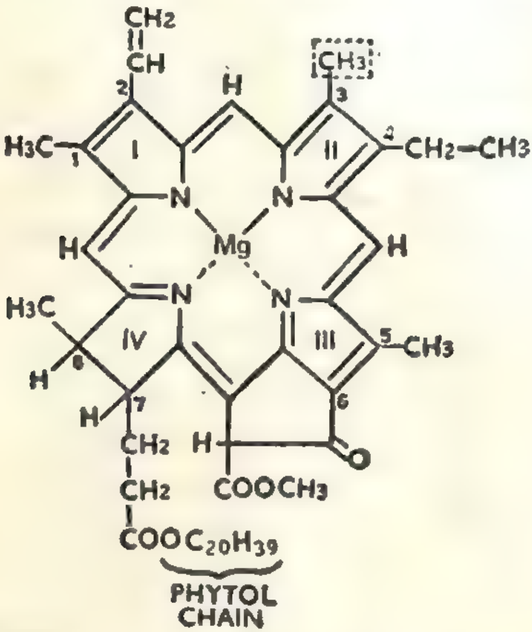


Fig. 50. Structural formula of chlorophyll a. The formula for chlorophyll b is the same except that there is $-CHO$ group in place of $-CH_3$ group enclosed in dotted square.

- Molecular structures of chloroyholl a and b are given in Fig. 50. Both of them consist of **Mg–Porphyrin 'head'** which is **hpydrophilic** and a **phytol 'tail'** which is **lipophilic**. The two chlorophylls differ because in chlorophyll b there is a $-CHO$ group instead of a $-CH_3$ group at the 3rd C atom in II pyrrol ring.

- Chlorophyll is formed from **protochlorophyll** in light. The protochlorophyll lacks two hydrogen atoms one each at 7th and 8th C atoms in IV pyrrole ring.

$$\text{Protochlorophyll} \xrightarrow[\text{2H}]{\text{Light}} \text{Chlorophyll}$$

(2) **Carotenoids** (Yellow or Orange Pigments)

(*i*) **Carotenes**

● These consist of an open chain conjuagated double bond system ending on both sides with **'ionone' rings**.

● They are **hydrocarbons** with a general molecular formula $C_{40}H_{56}$.

● Different carotenes differ only in the arrangement of their molecules in space i.e., they are **sterioisomers**. Structural formula of β-carotene is given below in Fig. 51.

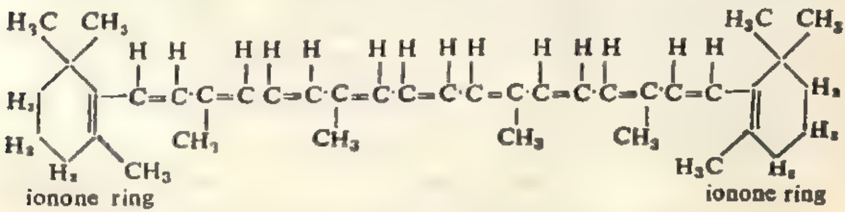


Fig. 51. Structural formula of β—carotene.

(*ii*) **Xanthophylls (Carotenols)**. These are similar to carotenes but differ in having **two oxygen atoms** in the form of hydroxyl, carbonyl, or carboxyl groups attached to the 'ionone' rings. Accordingly, their general formula is $C_{40}H_{56}O_2$

(3) **Phycobillins** (Red and Blue Pigments).

These consist of an **open** conjuagated system of four pyrrol rings and lack Mg and the phytol chain. The structure of the red pigment **phycoerythrobillin** is given below in Fig. 52.

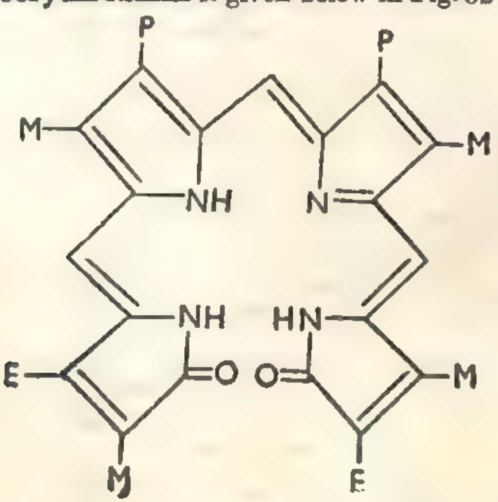


Fig. 52. Structure of phycoerythrobillin.
(M. methyl; E, ethyl; P, propionyl groups).

Location of Photosynthetic Pigments in Chloroplasts

The photosynthetic pigments are located in **grana** portions of the chloroplasts in higher plants. A number of molecular models

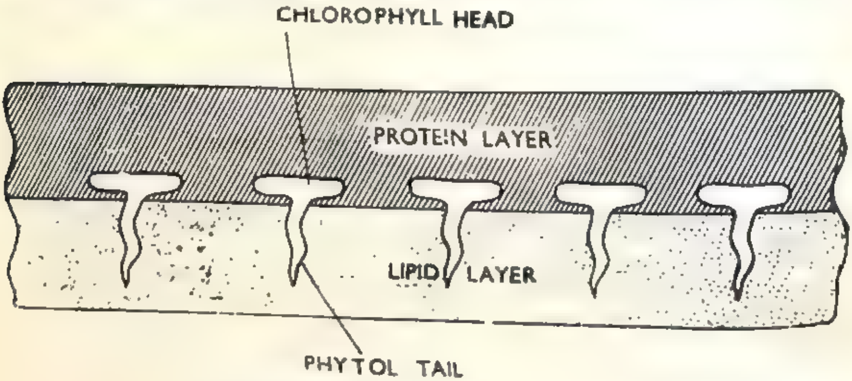


Fig. 53. A model showing monomolecular layer of chlorophylls in between protein and lipid layers of grana lamellae. (After Rabinowitch and Govindjee).

of the chloroplasts showing the arrangement of pigment molecules have been given by different workers from time to time and it is usually held that the chlorophyll molecules form a **monomolecular layer** between the alternative protein and the lipid layers in grana lamellae (thylakoids). The **hydrophilic 'heads'** of the chlorophyll molecules remain embedded in the protein layer while the **lipophilic phytol 'tails'** in the lipid layer (Fig. 53).

The other pigments are thought to be present along with the chlorphoyll molecules. **Weier and Benson** (1966, 1967) have also included chlorophyll molecules in the **fret membranes** (stroma lamellae) in their model of the chloroplasts.

Absorption and Utilisation of Light Energy by Photosynthetic Pigments.

- Chief source of light energy for photosynthesis is **sun**.

- The earth receives only about 40% (or about 5×10^{20} K. cal.) of the total solar energy. The rest is either absorbed by the atmosphere or is scattered into space.

- All the incident light energy falling on green parts of the plants is not absorbed and utilised by pigments. Some of the incident light is **reflected**, some is **transmitted** through them while only a small portion is absorbed by the pigments.

- Photosynthetic pigments absorb light energy only in the **visible part of the spectrum**. However, certain photosynthetic bacteria use **infra-red** light of comparatively shorter wavelengths. The spectrum of radiant energy is given in Fig. 54.

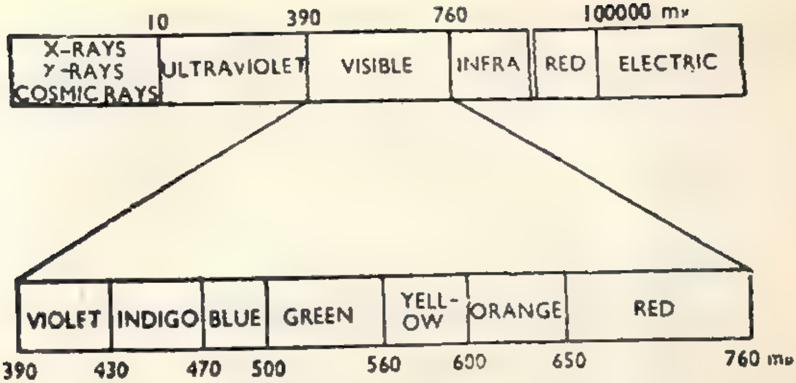


Fig. 54. Spectrum of radiant energy.

● Only about 1% of the total solar energy received by the earth is absorbed by the pigments and is utilised in photosynthesis.

● There is very weak absorption by pigments in green part of the spectrum and hence, the chloroplasts appear green in green plants.

Absorption Spectra of Chlorophylls. They chiefly absorb in the **violet-blue** and **red** parts of the spectrum. The absorption band shown by the chlorophylls in violet-blue region is also called as **soret band**. Characteristic absorption peaks shown by different chlorophylls both *in vivo** (*i.e.*, intact cell) and *in vitro** (*i.e.*, in solvents) are given below in Table 6.

Table 6. Absorption Peaks of Different Chlorophylls.

Type of Chlorophylls	Characteristic absorption Peaks	
	in vitro mμ	*in vivo* mμ
Chlorophyll a	410, 660	435, 670 680 (Several forms)
Chlorophyll b	452, 642	480, 650
Chlorophyll c	445, 625	645
Chlorophyll d	450, 690	740
Bacteriochlorophyll a	365, 605, 770	800, 850, 890
Bacteriochlorophyll b	368, 582, 795	1017
Bacterioviridin (two forms)	425, 650 432, 660	750 or 760

* *in vivo* = Within the living organisms.
in vitro = 'In glass' (vessel). But this term is usually applied to biological processes when they are experimentally made to occur in isolation from the whole organisms.

● Absorption spectra of different chlorophylls differ *in vivo and in vitro.*

● From the table on the previous page it is quite evident that **there are several forms of the chlorophyll a** *in vitro* showing a number of absorption peaks in the red part of the spectrum.

Absorption spectra of chlorophyll a and chlorophyll b (*in vitro*) are given in Fig. 55.

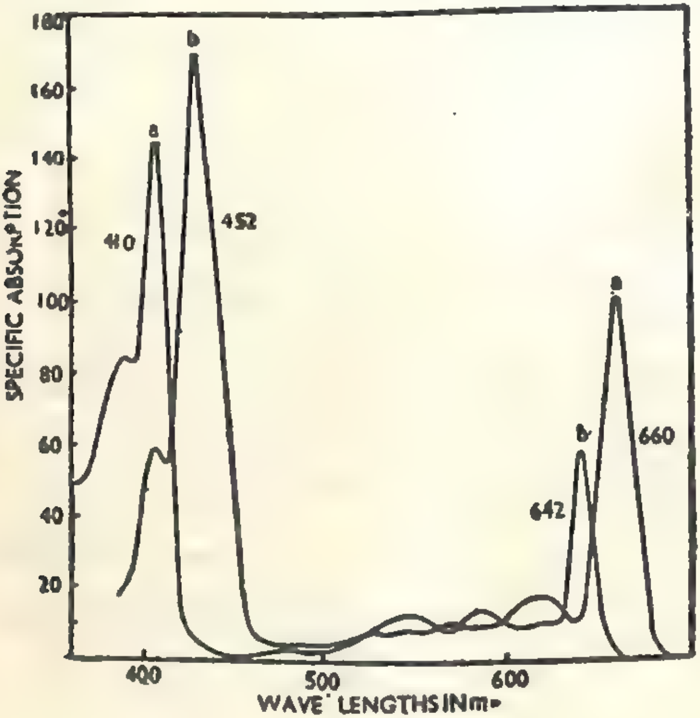


Fig. 55. Absorption spectra of chlorophyll a and b in ether solution.

Absorption Spectra of Carotenoids. These pigments absorb light energy in **blue, blue-green** and **green** parts of the spectrum.

Absorption Spectra of Phycobillins, See Table 7.

Table 7

Type of Phycobillins	Maximum Absorption
Phycoerythrins	In green part of the spectrum.
Phycocyanins	In orange part of the spectrum.
Allophycocyanin	In near red part of the spectrum.

Transfer of Light Energy Absorbed by Accessory Pigments to Chlorophyll a. All the pigments except chlorophyll a are called as **accessory pigments**. All the light energy absorbed by accessory pigments is transferred to **Chlorophyll a** molecule which alone can take part in primary photochemical reaction in photosynthesis. Chlorophyll a molecules also absorb light energy directly. However, in **photosynthetic bacteria** the above function is accomplished by **bacteriochlorophyll** and **bacterioviridin** because they do not have other types of pigments.

EXCITED STATES OF ATOMS OR MOLECULES, FLUORESCENCE AND PHOSPHORESCENCE

The normal state of the molecules or atoms is called as **ground state** or **singlet state**. When an electron of a molecule or atom absorbs a **quantum*** of light, it is raised to a higher energy level which is called as **excited second singlet state**. This is **unstable** and has a half-life of 10^{-12} seconds.

- The electron comes to the next higher energy level by the loss of some of its extra energy in the form of **heat**. This is called **excited first singlet state** and is also unstable with a half-life of 10^{-9} seconds.

- From the first singlet state the excited electron may return to the ground state in two ways : (*i*) either losing its remaining extra energy in the form of **heat**, or (*ii*) by losing extra energy in the form of **radiation energy**. The latter process is called as **fluorescence.** The substances which show this property of fluorescence emit fluorescent light **only during the period they are exposed to incident light**. Secondly, the **fluorescent light is of higher wave length than the incident light**. It is because some energy is lost during the change of excited second singlet state to excited first **singlet state**. (Light rays of higher wavelength have comparatively lower energy).

- The excited molecule or the atom may also lose its electronic excitation energy by '**internal conversion**' and comes to another excited state called as **triplet state** which is **metastable** with a half-life of 10^{-3} seconds. In this excited state the electron carrying extra energy can take part in further reaction.

- From the triplet state the excited molecule or the atom may return to the ground state in three ways : (*i*) by losing its remaining extra energy in the form of heat. (*ii*) by losing the extra

---

* Light rays consist of tiny particles called as **photons**. The energy carried by a photon is called as a **quantum** and is represented by $h\nu$. Light rays of shorter wavelengths contain more energy per photon of light than the light rays of longer wavelengths. For instance, one photon of blue light contains about 7(k. cal. of energy while one photon of red light contains about 40 k. cal. of energy.

energy in the form of radiant energy. This latter process is called as **phosphorescence** (Fig 56). The substances which show this property of phosphorescence emit phosphorescent light **even after the incident radiant light is cut-off.** Secondly, **the phosphorescent light is of higher wavelength than the incident light and also fluorescent light.** *(iii)* the electron carrying the extra energy may be expelled from the molecule and is consumed in some further chemical reaction and a fresh normal electron returns to the molecule, or the extra energy is utilised in the reaction and the same electron which has now become unexcited returns to the molecule. **This is**

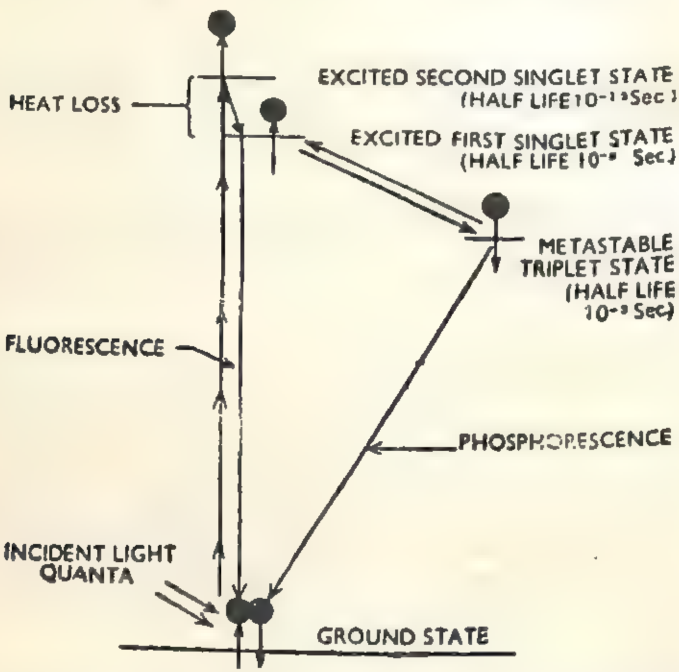


Fig. 56. Diagram to show excitation of molecules to fluorescence or phosphorescence.

what exactly happens with excited triplet state of Chlorophyll a molecule which takes part in primary photochemical reaction in photosynthesis.

Significance of the Phenomenon of Fluorescence in Photosynthesis.

The phenomenon of fluorescence has greatly helped in our understanding of the transfer of light energy in between the photosynthetic pigments by resonance. We know that different photosynthetic pigments are very closely packed. Some of them absorb light rays of shorter wavelength (with more energy) while others are capable of absorbing light rays of higher wavelength (with lesser

energy). They also possess property of fluorescence and it is not difficult to understand that the **fluorescence spectrum** of some of the pigments will overlap the **absorption spectrum** of some other pigments. In other words, the pigments which absorb light rays of shorter wavelengths will emit fluorescent light (of higher wavelengths) which in turn will be absorbed by other pigments which normally absorb light rays of higher wavelengths (See also Red drop and Emerson's enhancement effect, page 168).

QUANTUM REQUIREMENT AND QUANTUM YIELD

The number of photons (or quanta) required to release one molecule of oxygen in photosynthesis is called as **quantum requirement**. On the other hand, the number of oxygen molecule released per photon of light in photosynthesis is called as **quantum yield**. The quantum yield is always in fraction of one.

Warburg found minimum quantum requirement for photosynthesis to be **4**. It is because the reduction of one molecule of CO_2 by two molecules of H_2O requires the transfer of 4 H atoms. The transfer of each H atom from H_2O to CO_2 requiring one photon or quantum of light.

$$\begin{array}{rcl} 4H_2O & \rightarrow & 4OH^- + 4H^+ \\ 4OH^- & \rightarrow & 2H_2O + O_2 \\ 4H + CO_2 & \rightarrow & (CH_2O) + H_2O \\ \hline 2H_2O + CO_2 & \rightarrow & (CH_2O) + O_2 + H_2O \end{array}$$

(CH_2O) in the above equation represents 1/6 of the carbohydrate molecule such as glucose. One molecule of glucose contains about **686 k. cal**. of energy, therefore, **1/6** glucose molecule will contain **686/6**=app. **112 k. cal**. of energy. We also know that the rate of photosynthesis is maximum in red light and each photon of **red light** contains about **40 k. cal**. of energy. This would suggest that the efficiency with which the plants can convert light energy into chemical energy is $112/40 \times 4 = 70\%$ which indeed is very high. Warburg has even reported that *Chlorella* can carry out photosynthesis with a quantum requirement of only 2·8 *i.e.*, with cent per cent efficiency of converting light energy into chemical energy.

Warburg's findings have been severely criticised by **Emerson** and other workers. According to them photosynthesis is a very complicated process and is not so efficient as to convert all the light energy into chemical energy. There is a considerable loss of light energy absorbed during photosynthesis, therefore, the minimum quantum requirement for photosynthesis as suggested by them is **8—10** which is widely accepted at present.

Considering that the quantum requirement for photosynthesis is 8—10, the quantum yield would accordingly be 1/8 =0·125 to 1/10 =0·10.

RED DROP AND EMERSON'S ENHANCEMENT EFFECT

Robert Emerson while determining the quantum yield of photosynthesis in *Chlorella* by using monochromatic light of different wavelengths noticed a **sharp decrease** in quantum yield at wavelengths greater that **680 mμ**. Because this decrease in the quantum yield took place in the **red** part of the spectrum, the phenomenon was called as **red drop**.

Emerson and his co-workers later on found that the inefficient far-red light in *Chlorella* beyond 680 mμ can be made fully efficient

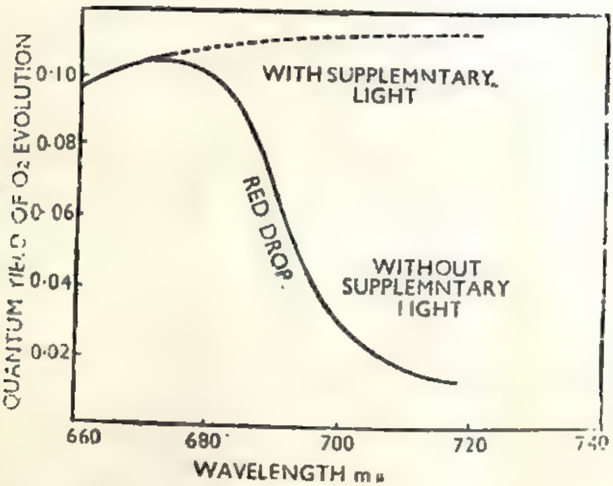


Fig. 57. Red drop and the Emerson's effect in *Chlorella*.

if supplemented with light of shorter wavelengths. The quantum yield from the two combined beams of light was found to be greater than the sum effect of both beams used separately. This enchancement of photosynthesis is called as **Emerson's enhancement effect** (Fig. 57).

TWO PIGMENT SYSTEMS

The discovery of red drop and the Emerson's enhancement effect has led scientists to suggest that photosynthesis is driven by **two photochemical processes**. These processes are associated with two groups of photosynthetic pigments called as **pigment system I** and the **pigment system II**. Wavelength of light shorter than 680 mμ affect both the pigment systems while wavelengths longer than 680 mμ affect only pigment system I.

- Pigment system I is relatively very weakly fluorescent while pigment system II is strongly fluorescent.

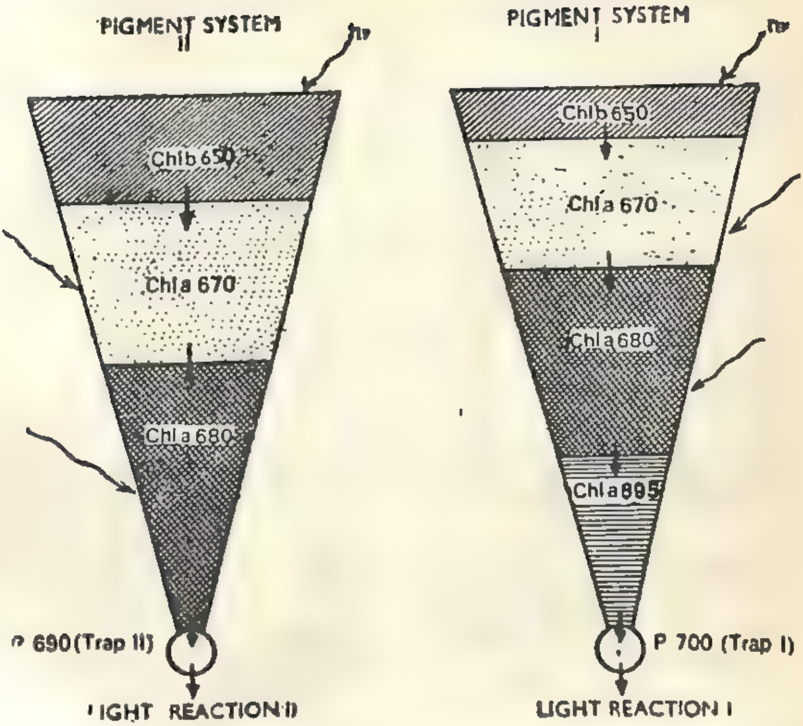


Fig. 58. A hypothetical scheme for the distribution of the chlorophylls in two pigment systems in green algae and higher plants. (After Govindjee, Papageorgiou, and Rabinowitch, 1967).

- In green plants, pigment system I contains chlorophyll b, chl. a 670, chl. a 680, chl. a 695 and a very small amount of a special form of chl. a absorbing at 700 mμ which is known as **P 700** and constitutes the **reaction centre** of pigment system I.

- The pigment system II contains chlorophyll b, chl. a 670 and chl. a 680. A special form of chl. a absorbing at 690 mμ and called as **P 690** constitutes the reaction centre of pigment system II.

- Carotenoids are present in both the pigment systems.

- In case of red and blue-green algae the pigment systems contain phycobillins in place of chlorophyll b.

- The relative proportion of chlorophyll b and different forms of the chlorophyll a is different in the two pigment systems (Fig. 58).

- Light energy absorbed by pigments in the two systems is ultimately **trapped** by the **P 700** and **P 690** forms of chlorophyll-a which alone can take part in further photochemical reaction.

PHOTOSYNTHETIC UNITS—THE QUANTASOMES

The work of **Emerson** and **Arnold** (1932) showed that about 2500 chlorophyll molecules are required to fix one molecule of CO_2 in photosynthesis. This number of chlorophyll molecules was called the **chlorophyll unit** but the name was subsequently changed to **photosynthetic unit**. However, since the reduction or fixation of one CO_2 molecule requires about 10 quanta of light, it is assumed that 10 flashes of light are required to yield one O_2 mol. or reduction of one CO_2 mol. Thus, each individual unit would contain 1/10 of 2500 *i.e.*, 250 molecules. It is the number **200—300** chlorophyll molecules per photosynthetic unit which is usually encountered in the literature and is considered as a **physiological unit of function**.

Steinman (1952) first observed certain granular structures in chloroplast lamellae under the electron microscope. These structures appeared more clearer in pictures obtained by **Park and Biggins** (1961). Later on, Park and Biggins (1964) suggested that these granular structures may be the **morphological expression of the physiological photosynthetic units** and called them as **quantasomes**.

Quantasomes measure 180 Å × 160 Å and are 100 Å thick. Work of Park and Biggins (1964) on the chemical composition of the quantasomes has revealed that one quantasome contains about **230** chlorophyll molecules. This is very close to the number of chlorophyll (200 – 300) contained in the physiological photosynthetic unit.

Although it is now certain that the arrangement of chlorophylls and other molecules is highly ordered within the grana lamellae or thylakoids, serious doubts have been expressed as to whether quantasomes do in fact represent the intact photosynthetic units.

MECHANISM OF PHOTOSYNTHESIS*

The process of photosynthesis is a complicated oxidation-reduction process resulting ultimately in the oxidation of water and reduction of CO_2. The mechanism of photosynthesis consists of two parts : (1) **Primary photochemical reaction** or **Light reaction or Hill's reaction** and (2) **Dark reaction** or **Blackman's reaction or Path of carbon in photosynthesis**. In Primary photochemical reaction **assimilatory power** (*i.e.*, **$NADPH_2$ + ATP**) is generated and O_2 is released. The assimilatory power is utilised in dark reaction in reducing CO_2 to carbohydrates.

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* Mechanism of photosynthes is discussed here is applicable to algae and higher plants. It differs in photosynthetic becteria which have only one pigment system (the functional equivalent of pigment system I).

(1) PRIMARY PHOTOCHEMICAL REACTION OR LIGHT REACTION OR HILL'S REACTION

Primary photochemical reaction which is faster than the dark reaction, takes place only **in presence of light** in the **grana** portions of the chloroplasts. It can be studied under the following heads :—

(i) Absorption of Light Energy by Chloroplast Pigments

Different chloroplast pigments absorb light in different regions of the visible part of the spectrum.

(ii) Transfer of Light Energy from Accessory Pigments to Chlorophyll a.

All the photosynthetic pigments except chlorophyll a are called as accessory pigments. The light energy absorbed by them is transferred by resonance to **chlorophyll a** which alone can take part in primary photochemical reaction. Chlorophyll a molecule can also absorb the light energy directly. In pigment system II the photoreaction centre is **P 690** while in pigment system I it is **P 700.**

(iii) Activation of Chlorophyll a Molecules by Photons of Light

When P 690 or P 700 forms of chlorophyll—a molecule in two pigment systems receives a **photon (qunatum)** of light it becomes an excited molecule having more energy than the ground state energy. After passing through the unstable **second singlet state** and **first singlet state**, the chlorophyll molecule comes to the **metastable triplet state** (For details see page 123). It is this latter excited form of chlorophyll a which in fact takes part further in primary photochemical reaction. It expels its energy along with an electron and a positive charge comes on the chlorophyll a molecule which now becomes oxidised.

$$\text{Chlorophyll a} \xrightarrow{\text{Light}} \text{Excited Triplet State of Chlorophyll a}$$

$$\text{Excited Triplet State of Chlorophyll a} \longrightarrow (\text{Chlorophyll a})^{+} + e^{-}$$

(iv) Photolysis of Water and O_2 Evolution (Oxidation of Water)

These are associated with pigment system II and are catalysed by the presence of **Mn^{++}** and **Cl^-** ions. When pigment system II is active *i.e.*, it receives light, the water molecules split into **OH^-** and **H^+** ions (photolysis of water). Its mechanism is least understood. The **OH^-** ions unite to form some water molecules again

and release O_2 and electrons. It is believed that photolysis of water involves a strong oxidant which is yet unknown and is designated as Z.

$$4H_2O \rightarrow 4H^+ + 4(OH^-)$$
$$4(OH^-) \rightarrow 2H_2O + O_2 + 4e^-$$

(v) Electron Transport and the Production of Assimilatory Power (*i.e.*, NADPH$_2$+ATP)

It has already been said that when chlorophyll a molecule receives a photon of light it becomes excited and expels the extra energy along with an electron in both the pigment systems. This electron after travelling through a number of electron carriers is either cycled back or is consumed in reducing **NADP** (Nicotinamide Adenine Dinucleotide Phosphate) to **NADPH$_2$**. The extra light energy carried by the electron is utilised in the formation of **ATP** molecules at certain places during its transport. This process of the formation of **ATP** from **ADP** and inorganic phosphate (iP) in photosynthesis is called as **photosynthetic phosphorylation** or **photophosphorylation**.

Arnon has contributed a lot in our understanding of the electron transport and photophosphorylation in chloroplasts. These are of two types :—

(a) **Non-cyclic Electron Transport and Non-cyclic Photophosphorylation.** This process of electron transport is initiated by the absorption of a photon (quantum) of light by P_{700} form of chlorophyll a molecule in **pigment system I** which gets excited. An electron is ejected from it so that an electron deficiency or a 'hole' is left in the P_{700} molecule (or in other words a positive charge comes on chlorophyll a molecule). This ejected electron is trapped by **FRS** (Ferredoxin reducing substance) which is an unknown oxidation—reduction system with a redox potential* (E'_0) of $-0{\cdot}6$ volts and

* The redox potential (E'_0) or the oxidation reduction potential is the potential required in a cell to produce oxidation at the anode and reduction at the cathode. This potential is measured relative to a standard hydrogen electrode which is taken as zero. The hydrogen electrode consists of platinum, over which hydrogen is bubbled, to produce a standard concentration of hydrogen ions.

Any compound which is capable of being reduced and oxidised forms a **redox system** and has a certain redox-potential (or E'_0) value. The latter is determined at a particular temp. and pH (usually 25°C and pH 7) and is expressed in terms of volts (V). The redox-system having high negative E'_0 value has high **'electron pressure'** and acts as **electron donor.** The electron in such system has more energy. On the other hand, a redox system having high positive or comparatively less negative E'_0 value has high **'electron affinity'** and acts as **electron acceptor.** The electron in such system has lower level of energy. During the transition of electron from donor to acceptor a portion of its energy is lost which in certain cases may be sufficient enough and can be stored in a chemically bound form as ATP.

may be a pteridene. The electron is now transferred to a non-heme iron protein called **ferredoxin** (Fd) with E'_0 of $-0{\cdot}432$ V. From ferredoxin the electron is transferred to NADP ($E'_0=-0{\cdot}32$ V) via the intermediate protein electron carrier *ferredoxin-NADP-reductase* so that NADP is reduced to **NADPH.**

Now, when a photon (quantum) of light is absorbed by P_{690} form of chloroplyll a molecule in **pigment system II** it gets excited and an electron is ejected from it so that an electron deficiency or a 'hole' is left behind in the P_{690} molecule. This ejected electron is trapped by a compound of unknown identity usually designated **Y**

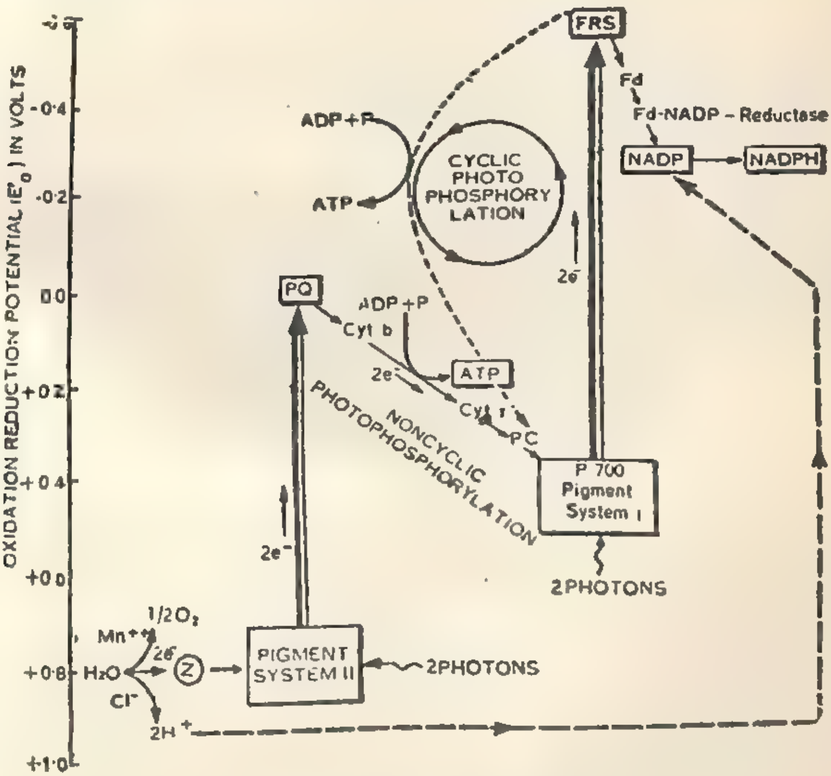


Fig. 59. Schematic representation of the electron transport and photophosphorylation in photosynthesis.

(Compound Y is sometimes called as **Q** because it also causes quenching of the characteristic fluorescence of chlorophyll a in pigment system II). This unknown compound forms oxidation-reduction system with a redox-potential (E'_0) value more negative than 0·0 V. From Y the electron passes **downhill** along a series of compounds or intermediate electron carriers and is ultimately received by

pigment system I where it 'fills the hole.' Redox potential of P_{700} in pigment system I is $+0{\cdot}43$ V. The series of compounds consists of (*i*) **plastoquinone (PQ)** whose chemical structure shows similarity with vitamins of **K** Series. It has a redox-potential (E'_0) of $+0{\cdot}113$ V, (*ii*) *cytochrome b-559* ($E'_0 = +0{\cdot}055$V), (*iii*) *cytochrome f* ($E'_0 = +0{\cdot}36$V) and (*iv*) **plastocyanin (PC)** which is a copper containing protein ($E'_0 = +0{\cdot}39$V). At one place during this electron transport *i.e.*, between *cytochrome b* and *cytochrome f* there is enough change in free energy which allows phosphorylation of one molecule of ADP to form one **ATP** moleeule (photophosphorylation).

The 'hole' in pigment system I has been filled by the electron coming from pigment system II. But the 'hole' or an electron deficiency is still there in pigment system II. This is fulfilled by the electron coming from photolysis of water. Water here acts as electron donor. It has redox-potential (E'_0) of $+0{\cdot}82$V. This transfer of electron from water probably involves a strong oxidant which is yet unknown and is designated as **Z**.

In the above scheme of electron transport the electron ejected from pigment system II did not return to its place of origin, instead it was taken by pigment system I. Similarly, the electron ejected from pigment system I did not cycle back and was consumed in reducing NADP. Therefore, this electron transport has been called as **non-cyclic electron transport** and the accompanying photophosphorylation as **non-cycle photophosphorylation**.

Non-cyclic photophosphorylation and O_2 evolution are inhibited by 3-(4′-chlorophenyl)-1, 1-dimethylurea (**CMU**) and 3-(3′4′-dichlorophenyl)-1, 1-dimethylurea (**DCMU**).

(In the electron transport system described above we have considered the transport of only one electron because P_{700} and P_{690} molecules in pigment systems I & II respectively can give or take only one electron at a time. But the reduction of one molecule of NADP ($NADP^+ \rightarrow NADPH + H^+$) requires 2 electrons and 2 protons. Therefore, two molecules of P_{700} are excited by 2 photons (quanta) of light to release 2 electrons which reduce NADP. Similarly, two photons will release 2 electrons from two molecules of P_{690} which in turn will be taken by two molecules of P_{700} in pigment system I. On the other hand, photolysis of one molecule of H_2O results in the production of 2 electrons, 2 protons and $\frac{1}{2}O_2$. These 2 electrons thus produced will fill the holes, of two molecules of P_{690} in pigment system II while 2 protons (H^+) will be utilised in the reduction of NADP. Thus, 4 photons and one water molecule are reduired to reduce one molecule of $NADP^+$.

Like P_{700} and P_{690} molecules, the cytochromes and plastocyanin involved in electron transport also have only one electron transition. Plastoquinone on the other hand has 2 electron transition *i.e.*, it can either give or take 2 electrons at one time.)

(b) Cyclic Electron Transport and Cyclic Photophosphorylation :

In contrast to non-cyclic electron transport, the cyclic electron transport involves only **pigment system I** and takes place under conditions which exclude non-cyclic photophosphorylation. This situation is created if the activity of pigment system II is blocked. The latter can be accomplished by the use of specific inhibitors or by using wavelengths of light greater then 680 mμ. Under these conditions (*i*) only pigment system I remains active (*ii*) photolysis of water does not take place (*iii*) blockage of non-cyclic ATP formation causes a drop in CO_2 assimilation in dark reaction and (*iv*) there is a consequent shortage of oxidised NADP.

Thus, when P_{700} molecule is excited in pigment system I by absorbing a photon (quantum) of light, the ejected electron is captured by *ferredoxin* ($E'_0 = -0{\cdot}432V$) via FRS. From *ferredoxin* the electron can not be drained off to the dark reactions of photosynthesis through oxidised NADP (due to the shortage of latter) and ultimately it falls back to the P_{700} molecule ($E'_0 = +0{\cdot}43V$), involving of course a number of other intermediate electron carriers of redox system. These are **probably** *cytochrome b_6* ($E'_0 = -0{\cdot}06V$), *cytochrome f*($E'_0 = +0{\cdot}36V$) and plastocyanin ($E'_0 = +0{\cdot}39V$). It is quite obvious from the E′ values that all these intermediate electron carriers form an electrochemical gradient of decreasing negative values which facilitates the downhill transport of electron from FRS to P_{700} molecule. At two places during this electron transport *i.e.*, between *ferredoxin* and *cytochrome b_6* and *cytochrome f* there is phosphorylation of one ADP molecule to form one ATP molecule.

Because in the above electron transport system the electron which was ejected from P_{700} molecule is cycled back, the process has been called as **cyclic electron transport** and the accompanying phosphorylation as the **cyclic photophosphorylation**.

Significance of Cyclic Photophosphorylation

We have seen that during cyclic electron transport and phosphorylation photolysis of water, O_2 evolution and reduction of NADP do not take place. It generates only ATP molecules and as such can not drive dark reactions of photosynthesis. On the other hand non-cyclic photophosphorylation does not produce sufficient ATP in relation to NADPH to operate the dark phase of photosynthesis (Calvin Cyclic). Therefore, the deficiency of ATP molecules in non-cyclic photophosphorylation is made up by the operation of cyclic photophosphorylation instead of the former for certain periods. Secondly, cyclic photophosphorylation may be an important process in providing ATP for synthetic processes (other than photosynthesis) *e.g.*, synthesis of starch, proteins, lipids, nucleic acids, pigments within the Chloroplasts.

Table-8. MAIN POINTS OF CYCLIC AND NON-CYCLIC ELECTRON TRANSPORT AND PHOTOPHOSPHORY LATION IN CHLOROPLASTS

Cyclic Electron Transport and Photophosphorylation	Non-Cyclic Electron Transport and Photophosphorylation
1. Associated with pigment system I.	1. Associated with both pigment system I and II.
2. The electron expelled from chlorophyll molecule is cycled back.	2. The electron expelled from chlorophyll molecule is not cycled back. Its loss is compensated by electron coming from photolysis of water.
3. Photolysis of water and evolution of O_2 do not take place.	3. Photolysis of water and evolution of O_2 take place.
4. Phosphorylation takes place at two places.	4. Phosphorylation takes place only at one place.
5. NADP it not reduced	5. NADP is reduced to $NADPH_2$

Thus we have seen that the light energy has been converted into chemical energy during primary photochemical reaction and is trapped in **ATP** and **$NADPH_2$** molecules. This chemical energy is finally stored in carbohydrate molecules when **ATP & $NADPH_2$** (*i.e.* the assimilatory power) are utilised in dark reaction of photosynthesis in reducing CO_2 to carbohydrates.

(2) THE DARK REACTION OR BLACKMAN'S REACTION OR THE PATH OF CARBON IN PHOTOSYNTHESIS

The dark reaction of photosynthesis is purely **enzymatic** and slower than the primary photochemical reaction. It takes place in **stroma** portion of the chloroplast and is **independent of light** *i.e.*, it can occur either in presence or in absence of light.

The conversion of CO_2 to carbohydrate with the help of **assimilatory power** ($NADHP_2$+ATP) in dark reaction of photosynthesis is most thoroughly analysed part of photosynthesis. This success had been due to the availability of a long lived radioactive isotope of carbon* C^{14} with a half-life of 5720 years. Main credit for investigating the sequences of dark reaction in photosynthesis goes to **Melvin Calvin** who was rewarded by the Nobel Prize in 1961. **A.A. Benson, J. Bassham** and other co-workers have also contributed a lot.

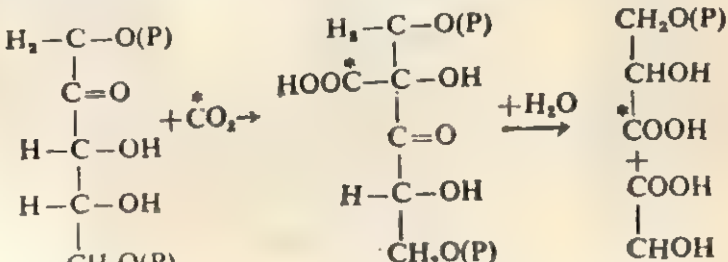
*This was discovered by Ruben and Kamen in 1940.

By employing C^{14} labelled carbon dioxide ($C^{14}O_2$) in photosynthesis and observing the appearance of characteristic radiations in different reaction intermediates and products in different experiments, **Calvin** and his co-workers were able to formulate the complete metabolic path of carbon assimilation in the form of a cycle which is called as **Calvin Cycle.**

THE CALVIN CYCLE (C_3 —PATHWAY)

Various steps of the Calvin-cycle which has also been shown in Fig. 60, are as follow :

(i) The CO_2 is accepted by **ribulose 1, 5-diphosphate** already present in the cells and a **6-carbon addition compound** is formed which is unstable. It soon gets converted into 2 molecules of **3-phosphoglyceric acid** due to hydrolysis and dismutation. Both these reactions take place in the presence of *carboxydismutase*. 3-phosphoglyceric acid is the **first stable product of dark reaction of photosynthesis.**



Ribulose 1, 5-diphosphate — 6-C-Addition compound — 3-phosphoglyceric acid

(ii) 3-Phosphoglyceric acid is reduced to **3-Phosphoglyceraldehyde** by the assimilatory power (generated in light reaction) in the presence of *triose phosphate dehydrogenase*. This reaction takes place in two steps :

3-Phosphoglyceric acid — 1, 3-Diphosphoglyceric acid

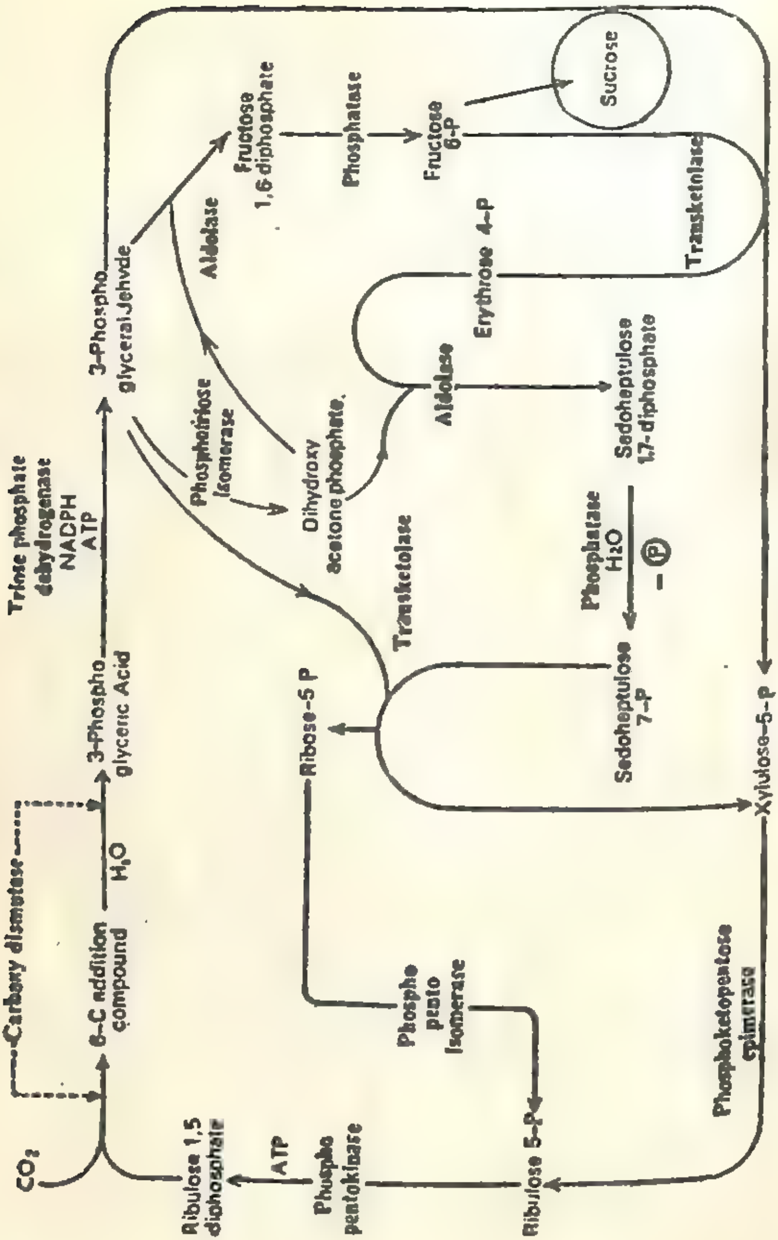
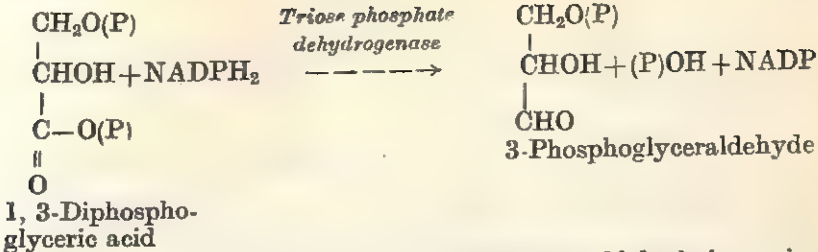
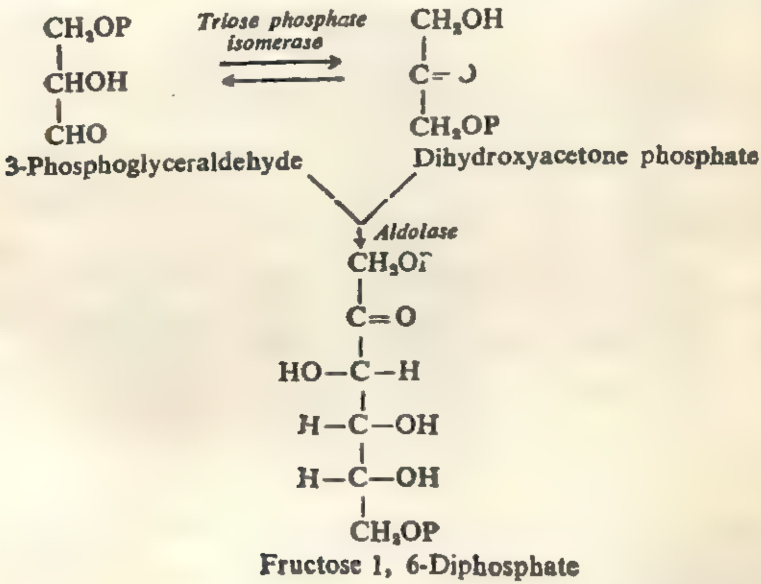


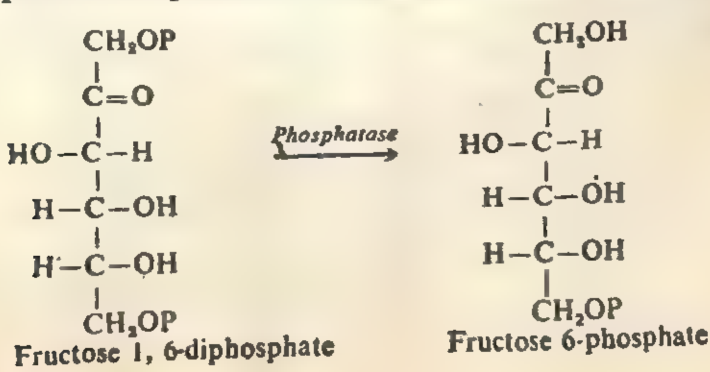
Fig. 60. The Calvin cycle.



(iii) Some of the molecules of 3-phoshoglyceraldehyde isomerise into **dihydroxyacetone phosphate**, both of which then unite in the presence of the enzyme *aldolase* to form **fructose 1, 6-diphosphate**.



(iv) Fructose 1,6-diphosphate is converted into **Fructose 6-phosphate** in the presence of *phosphatase*.



(v) Fructose-6-phosphate (hexose sugar) can easily be converted into a number of other carbohydrates such as **glucose, sucrose, starch** etc.

(vi) Some of the molecules of 3-phosphoglyceraldehyde produced in step (ii) instead of forming hexose sugars, are diverted to **regenerate** ribulose 1, 5-diphosphate in the system as follow :—

(vii) 3-Phosphoglyceraldehyde reacts with fructose-6-phosphate in the presence of the enzyme *transketolase* to form **erythrose-4-phosphate** (4-C atoms sugar) and **xylulose-5-phosphate** (5-C atoms sugar).

(viii) Erythrose-4-phosphate combines with dihydroxyacetone phosphate in the presence of the enzyme *aldolase* to form **Sedoheptulose 1,7—diphosphate** (7-C atoms sugar).

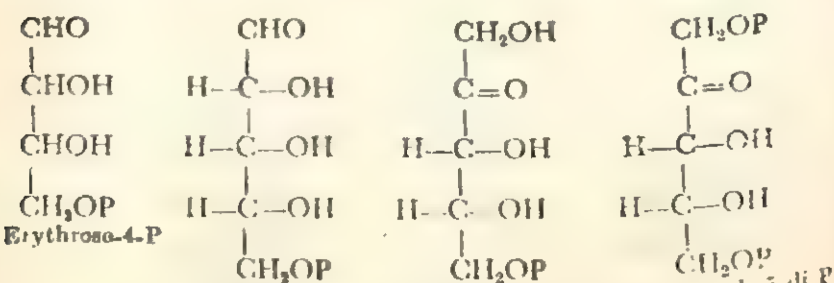
(ix) Sedoheptulose 1, 7-diphosphate looses one phosphate group in the presence of *phosphatase* to form **sedoheptulose-7 phosphate**.

(x) Sedoheptulose-7-phosphate reacts with 3-phosphoglyceraldehyde in the presence of *transketolase* to form **xylulose 5-phosphate** and **ribose-5-phosphate** (both 5-carbon atoms sugars).

(xi) Xylulose-5-phosphate is converted into another 5-C atoms sugar **ribulose-5-phosphate** in the presence of the enzyme *phosphoketopentose epimerase.*

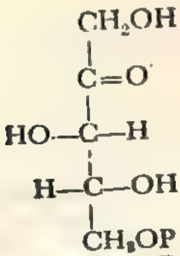
(xii) Ribose-5-phosphate is also converted into ribulose-5-phosphate. The reaction is catalysed by *phosphopentose isomerase.*

(xiii) Ribulose-5-phosphate is finally converted into **ribulose 1, 5-diphosphate** in the presence of *phosphopentose kinase* and **ATP.** thus completing the Calvin cycle.

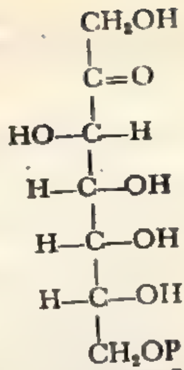


Erythrose-4-P　Ribose-5-P　Ribulose-5-P　Ribulose 1, 5-di P

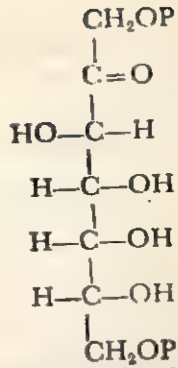
Fig. 61. Structural formulae of 4, 5 and 7-C atoms sugar phosphates involved in the Calvin cycle. (Contd.)



Xylulose-5-P



Sedoheptulose-7-P



Sedoheptulose 1, 7-di P

Fig. 61.. Contd. Structural formulae of 4, 5 and 7-C atoms sugar phosphates involved in the Calvin cycle.

Structural formulae of various 4, 5 and 7-C atoms sugars inovlved in the Calvin cycle are given in Fig. 61.

Because first visible product of this cycle is 3-phosphoglyceric acid which is a 3-C compound, Calvin cycle is also known as C_3-pathway.

EVIDENCES FOR THE EXISTENCE OF LIGHT AND DARK REACTIONS IN PHOTOSYNTHESIS

(1) Experiments with Intermittent Light

The rate of photosynthesis has been found to be greater in intermittent light (*i.e.*, light given after intervals of dark periods) than in continuous light. It indicates the existence of two stages in photosynthesis *i.e.*, a light and another dark. The light reaction is faster than the dark reaction. In continuous light the products of the light reaction (*i.e.*, $NADPH_2$ + ATP) are not consumed at the same rate in subsequent dark reaction at which they are produced in light reaction resulting in their accumulation. But with intermittent light the products of light reaction are consumed to fix CO_2 to carbohydrates both during the light period and the interval of dark period. Accumulation of $NADPH_2$ + ATP is prevented because they are not produced during dark periods.

(2) Temperature Coefficients

The ratio of the rate of a particular process at a certain temperature to the rate of that process exactly at 10°C lower is called as **temperature coefficient** and is denoted by Q_{10}. For purely chemical processes the value of Q_{10} is 2 or more *i.e.*, the rate of the process will become double or more by raising the temperature by 10°C. But for photochemical reactions Q_{10} is approximately one.

Blackman has observed that if the leaves were well illuminatedand received an ample supply of CO_2, the value of Q_{10} for photo-

synthesis was 2 or more. But in poorly illuminated leaves Q_{10} was 1. These results support the existence of a purely chemical reaction *i.e.*, the dark reaction and a photochemical reaction *i.e.*, the light reaction in photosynthesis.

(3) Physical Separation of the Light and Dark Reactions

Experiments have been successful in separating **grana** and **stroma** portions of the chloroplasts. If the isolated grana are illuminated in presence of suitable H-acceptors and in complete absence of CO_2, oxygen is released and assimilatory power is generated. The latter when supplied to stroma portion in the presence of CO_2 and even in complete absence of light resulted in the production of carbohydrates. These expriments clearly indicate the existence of a light dependent reactoin (localised in grana) and a light independent reaction or dark reaction (localised in stroma) in photosynthesis.

SOURCE OF OXYGEN RELEASED IN PHOTOSYNTHESIS

Before 1930's it was thought that O_2 released in photosynthesis comes from CO_2. But the idea that O_2 comes from H_2O and not from CO_2 which is now well established was first given by **Van Niel** (1930-31). He observed that in certain photosynthetic bacteria such as **green sulphur bacteria**, oxygen is not released during photosynthesis. Such bacteria instead of utilising H_2O make use of H_2S and liberate sulphur.

$$2H_2S + CO_2 \xrightarrow[\text{Light}]{\text{Green Sulphur Bacteria}} 2S + \underset{\substack{\text{Represents}\\\text{carbohydrate}}}{(CH_2O)} + H_2O$$

This prompted him to think that as sulphur comes from H_2S in green sulphur bacteria in photosynthesis, similarly, oxygen must come from H_2O in algae and higher plants and proposed a general formula for photosynthesis.

$$2H_2A + CO_2 \xrightarrow{\text{Light}} 2A + (CH_2O) + H_2O$$

In the above formula A will represent sulphur in case of green sulphur bacteria while in algae and the other higher green plants it will represent oxygen.

The idea of **Van Niel** was greatly supported by the experiments of **Hill** (1937) and isotopic studies done by **Ruben** and **Kamen** (1943).

Hill observed that if the isolated chloroplasts were illuminated in complete absence of CO_2 but in presence of suitable **H-acceptors** **(Hill's oxidants)** such as **indophenols** and **ferric salts**, oxygen was released.

Ruben and **Kamen** using a heavy isotope of oxygen (O^{18}) showed that if the photosynthesis took place in presence of H_2O^{18} and normal CO_2, the oxygen was found to be isotopically labelled.

$$2H_2O^{18}+CO_2 \longrightarrow O_2^{18}+(CH_2O)+H_2O$$

But if normal H_2O and CO_2^{18} were supplied, the O_2 evolved during photosynthesis did not contain the heavy isotope.

$$2H_2O+CO_2^{18} \longrightarrow O_2+(CH_2O^{18})+H_2O$$

C_4-DICARBOXYLIC ACID PATHWAY (HATCH–SLACK PATHWAY)

For considerable period of time the Calvin cycle as described earlier was thought to be the only photosynthetic reaction sequence operating in higher plants and algae. But in 1965 **Kortschak**, **Hartt** and **Burr** reported that 4-C containing dicarboxylic acids, **malate** and **aspartate** were the major labelled products when sugarcane leaves were allowed to photosynthesize for short periods in $C^{14}O_2$. This finding was confirmed and greatly elaborated by **Hatch** and **Slack** who observed heavy labelling of oxaloacetate, malate, and aspartate only when sugarcane leaves were exposed to $C^{14}O_2$ for 1 sec. Longer exposures resulted in decrease of of radio-activity in these acids with simultaneous increase in 3-phosphoglyceric acid, hexose monophosphates and sucrose. This and further studies by these workers led to the establishment of yet another CO_2 reduction pathway which is called as **Hatch-Slack pathway** and because C_4-dicarboxylic acids are the earliest products it is also called as C_4-dicarboxylic acid pathway.

Besides sugarcane leaves this pathway has been found to operate in many plant species of the family **Gramineae** *e.g.*, maize, sorghum etc. which are grouped together as '**tropical grasses**' and other plants *e.g.*, *Atriplex Amaranthus* etc. These are all known as **C_4 plants** and are distinguished by (i) absence of photo-respiration and (ii) anatomical similarities of leaf ('cane type'). In the leaves of these plants the vascular bundles are surrounded by **bundle sheath** of larger parenchymatous cells which in turn are surrounded by smaller **mesophyll** cells. Moreover, the chloroplasts in cells of bundle sheath are larger and usually lack grana ; the chloroplasts in mesophyll cells are smaller and always contain grana. These two types of chloroplasts may even be separated from one another by density gradient centrifugation. In maize and sugarcane **plasmodesmata** have been observed which connect cells of bundle sheath with adjacent mesophyll cells.

Various step of Hatch-Slack pathway (Fig. 62) which involves **two carboxylation reactions** one taking place in chloroplasts of

mesophyll cells and another in chloroplasts of cells of bundle sheath are as follow :—

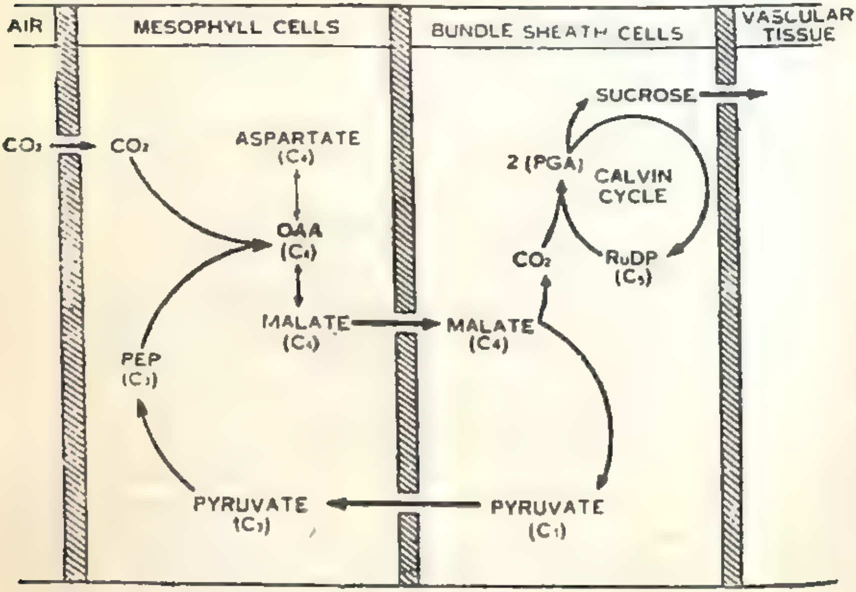
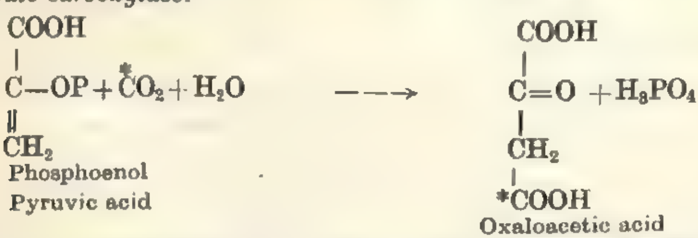
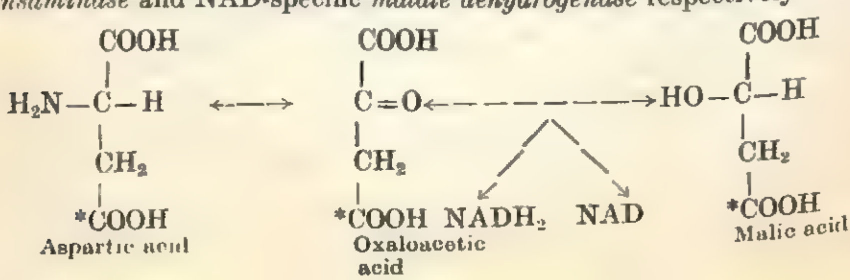


Fig. 62. Hatch-Slack Pathway of CO_2 fixation.
(PEP=Phosphoenol pyruvic acid ; OAA=Oxaloacetate ; RuDP=Ribulose di-phosphate ; PGA=Phosphoglyceric acid).

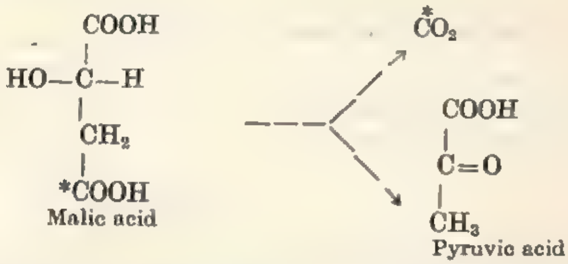
(i) The first step involves the carboxylation of phosphoenol pyruvic acid in chloroplasts of mesophyll cells to form C_4-dicarboxylic acid, oxaloacetic acid. This reaction is catalysed by ***phosphoenol pyruvate carboxylase.***



(ii) Oxaloacetic acid readily equilibriate with other C_4-dicarboxylic acids, aspartic acid and malic acid in the presence of enzymes *transaminase* and NAD-specific *malate dehydrogenase* respectively.

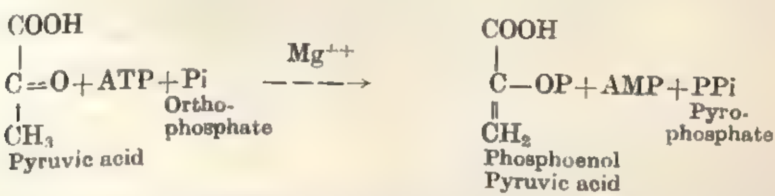


(iii) From chloroplasts of mesophyll cells the malic acid is transferred to the chloroplasts of bundle sheath cells where it is decarboxylated to form CO_2 and pyruvic acid in the presence of a NADP specific *malic enzyme*.



(iv) Now second carboxylation occurs in chloroplasts of bundle sheath cells. Ribulose-diphosphate accepts CO_2 produced in step (iii) in the presence of *carboxydismutase* system and ultimately yields 3-phosphoglyceric acid as in case of Calvin cycle. Some of the 3-phosphoglyceric acid is utilised in the formation of hexose monophosphates and sucrose while rest regenerates ribulose-diphosphate in the system (see Calvin cycle).

(v) The pyruve acid produced in step (iii) is transferred to chloroplasts of mesophyll cells where it is phosphorylated to regenerate phosphoenol pyruvic acid. This reaction is catalysed by *pyruvate Pi kinase*.



The enzymes catalysing reactions in chloroplasts of mesophyll cells are not found in chloroplasts of bundle sheath cells and *vice versa*.

Hatch-Slack pathway begins with the carboxylation of phosphoenol pyruvate and not of ribulose-disphosphate. It is because the former has great affinities with CO_2 than the latter.

In contrast to the C_4 plants, the other higher plants lack Hatch-Slack pathway and have only Calvin cycle (C_3-pathway) for the fixation of CO_2 in photosynthesis. these are called as **C_3 plants** and have only one type of chloroplasts.

Significance of Hatch-Slack Pathway :

The significance of this pathway is not clearly understood. But it has been suggested that (*i*) this pathway is a modification of Calvin cycle and is advantageous to plants growing in dense, stands of

tropical vegetation where the CO_2 concentration may be very much reduced, (*ii*) there has been a reduction of atm. CO_2 concentration since the evolution of photosynthesis and this might have prompted C_4 plants to select this pathway. (*iii*) the discovery of this pathway has indicated the existence of yet undiscovered photosynthetic reactions other than the conventional Calvin cycle.

DIFFERENCES BETWEEN C_3 & C_4 PLANTS

C_3 – Plants	C_4 – Plants
1. Examples of these plants are wheat, oats, barley, rice, cotton, beans, spinach, sunflower, *chlorella* etc.	1. Examples of these plants are sugarcane, maize, sorghum, *Atriplex*, *Amaranthus* etc.
2. Carbon pathway in photosynthesis is C_3—pathway *i.e.*, **calvin cycle**.	2. Carbon pathway in photosynthesis is C_4—Dicarboxylic acid pathway (**Hatch-slack pathway**).
3. First stable product of above carbon pathway is 3-C compound **phosphoglyceric acid (PGA)**.	3. First stable product of above carbon pathway is 4 – C compound **Oxaloacetic acid (OAA)**.
4. The leaves have diffused mesophyll and only one type of chloroplasts.	4. The leaves have 'cane type' of anatomy with compact mesophyll around the vascular bundles (bundle sheath) and dimorphic chloroplasts. Those of bundle sheath are large and lack grana, while those of mesophyll are smaller and contain grana.
5. Optimum temp. for photosynthesis is low to high.	5. Optimum temperature for photosynthesis is high.
6. **Photorespiration** occurs.	6. **No photorespiration**.
7. Photosynthetically less efficient.	7. Photosynthetically more efficient.
8. Carbon dioxide compensation point is high, 15 to 150 ppm.	8. Carbon dioxide compensation point is low even O ppm.
9. Rate of CO_2 evolution in light is higher.	9. Rate of CO_2 evolution in light is apparently none.
10. Carbonic anhydrase activity is high.	10. Carbonic anhydrase activity is low.
11. Rate of translocation of end products of photosynthesis is low.	11. Rate of translocation of end products of photosynthesis is high.
12. Optimum temperature for growth is low to high.	12. Optimum temperature for growth is high.

BLACKMAN'S LAW OF LIMITING FACTORS

Previously it had been customary to study the effect of individual factors on the rate of photosynthesis in terms of **minimum**, **optimum** and **maximum** (the three cardinal points). Earlier investigators could not realise the importance of simultaneous effect of different factors upon the rate of photosynthesis and obtained different values for these cardinal points under different conditions. For example, they found the optimum CO_2 concentration to be greater at high light intensities than at low light intensities.

This problem was first tackled satisfactorily by **F. F. Blackman** who in 1905 enunciated **law of limiting factors**. He states that "When a process is conditioned as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the 'slowest' factor". To explain his principle, Blackman gave the following illustration which is also shown diagrammatically in Fig. 63.

Suppose a leaf is exposed to a .ertain light intensity which can utilize 5 mg. of CO_2 per hour in photosynthesis. If only 1 mg. of CO_2 enters the leaf in an hour, the rate of photosynthesis is limited due to CO_2 factor. But as the concentration of the CO_2 increases from 1 to 5 mg./hour the rate of photosynthesis is also increased alodg the line AB. Any further increases in the CO_2 concentration will have no effect on the rate of photosynthesis which has become. constant along the line BC. It is because the low light intensity has become a limiting factor. Now the rate of photosynthesis will increase further along the line BD only if the intensity of light is also increased from low to a medium. At point D, the medium light intensity again becomes limiting factor and the rate of photosynthesis will again become constant along the line DE. In the same way, at still higher light intensity an increase in CO_2 will bring about an increase in the rate of photosynthesis along the line DF. And after the point F when the higher light intensity also becomes a limiting factor, further increase in CO_2 concentration will have no favourable effect on the rate of photosynthesis which becomes constant along the line FG.

Thus it is quite evident from the above illustration that the rate of photosynthesis can not be increased by increasing only one factor. The other factors should also be increased in proper proportion for favourable effect. Besides CO_2 and light, other factors which affect rate of photosynthesis such as temperature, water etc. may also become limiting factors under certain conditions.

Blackman's law of limiting factors is applicable to any physiological process which is affected by more than one factors.

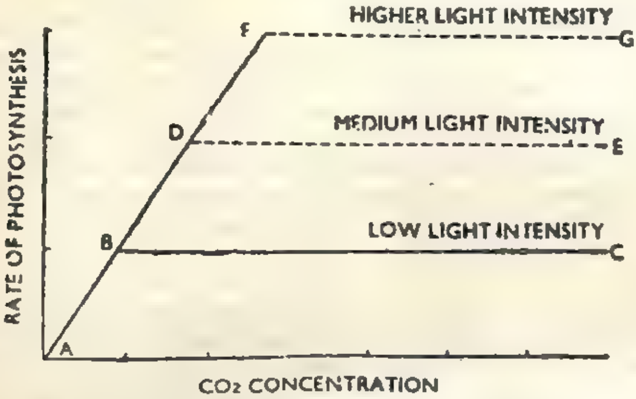


Fig. 63. Diagram to illustrate Blackman's law of limiting factors.

While explaining the principle of limiting factors it should be clearly borne in mind that the **absolute magnitude** of the factors is not so important as their **relative magnitude**. A factor which is present in smallest amount may not be limiting because its requirement may be in traces. On the other hand, another factor present in larger amount may become a limiting factor because its requirement for the physiological process might have been higher. And once the rate of a process has become constant due to a limiting factor, the rate of that process can only be increased by increasing only that factor which is limiting and none else.

Criticism of the Blackman's Law of Limiting Factors. In his illustration of the principle of limiting factors Blackman showed **abrupt breaks** in the rate of photosynthesis along the line BC, DE and FG (Fig. 63) after the particular light intensity had become a limiting factor. This has been criticised by many workers such as **James, Harder** and others. According to them the rate of photosynthesis declines **gradually** and not abruptly whenever a factor has become limiting. It is because all the chloroplasts are not under similar environmental conditions at any given time. Some of them might be receiving more light than the others which are deep seated in the leaves. Similarly, some of them might be receiving more CO_2 than the others. Therefore, if light or CO_2 factors have become limiting for photosynthesis in only some chloroplasts, that factor will not be limiting to the remaining chloroplasts and hence, the total rate of photosynthesis will decline gradually and not abruptly. Under such conditions more than one factors may become limiting simultaneously.

FACTORS AFFECTING PHOTOSYNTHESIS

The rate of photosynthesis is affected by a number of external and internal factors. The principle of limiting factors should be kept in mind while studying the effect of various factors on photosynthesis.

(A) EXTERNAL FACTORS

1. Light

In nature the chief source of light for photosynthesis in green plants is sun-light. Moon light has been found to be effective in marine algae. Besides these, any kind of artificial light *e.g.*, electric light can induce photosynthesis in green plants, provided it is in the visible part of the spectrum. The light is an essential factor for photosynthesis. It affects the rate of photosynthesis in three ways :—

(i) **Light Quality**. Photosynthesis in green plants takes place only in the **visible part of the spectrum** of light.* Although the light rays of longer wavelengths have lower energy than the light rays of shorter wavelengths, but owing to the heavy absorption in the red part of the spectrum by chlorophylls, maximum photosynthesis takes place in **red light**. The next highest rate of photosynthesis takes place in **blue light** while in **green light** it is minimum.

The rate of photosynthesis is higher in white light than in monochromatic light (*i.e.*, light rays of a particular wavelength).

(ii) **Light Intensity**. Usually the rate of photosynthesis is greater in intense light than in diffused light. But certain plants require less intense light for optimum photosynthesis and grow in shady places. They are called as **sciophytes**. On the other hand, the plants which grow in sunny places require more intense light for optimum photosynthesis. They are called as **heliophytes**.

Extremely intense light may have a direct inhibitory effect on **photosynthesis**, a phenomenon called as **solarization**. During solarization **photo-oxidation** of cellular components including the photosynthetic apparatus takes place which may even result in their death. Secondly, in extremely intense light other factors may soon become limiting thus reducing the rate of photosynthesis.

(iii) **Duration of Light**. Even a brief flash of light is enough for photosynthesis to occur. However, the rate of photosynthesis is greater in **intermittent light** than in **continuous light**. It is because in continuous light the **assimilatory power** accumulates and is not consumed in the dark reaction at the same rate at which it is produced in light reaction.

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*Certain photosynthetic bacteria also use infra-red light of comparatively shorter wavelengths.

2. CO_2

CO_2 constitutes about 0·03% by volume of the atmosphere. An increase in CO_2 concentration up to about 1% increases the rate of photosynthesis. But very high conc. may prove toxic and the rate of photosynthesis will go down.

3. Temperature

Different plants have different requirement of temperature for photosynthesis. For example, photosynthesis will stop in many plants at about freezing point but in some conifers it takes place even at—35°C. Similarly, temperatures beyond 40—50°C retard photosynthesis in most of the plants but certain xerophytes like *Opuntia* and algae growing in hot springs carry on photosynthesis even at 55°C and 75°C respectively.

Usually, an increase in temperature from 10°C to about 40°C brings about an increase in the rate of the photosynthesis. $\mathbf{Q_{10}}$ for photosynthesis is 2.

4. Water

Water is one of the raw materials and an essential factor for photosynthesis. Usually the water rarely acts as a limiting factor for photosynthesis but the rate of photosynthesis may go down if the plants are inadequately supplied with water.

5. O_2

See Warburg's effect.

(B) INTERNAL FACTORS

1. Chlorophyll Content

Chlorophyll is essential for photosynthesis. In etiolated plants and the non-green parts of variegated leaves in some plants photosynthesis does not take place. Although there are conflicting views regarding the direct relationship between chlorophyll content and the rate of photosynthesis, but theoretically it is quite obvious that the rate of photosynthesis should increase with an increase in the chlorophyll content provided the other factors are also favourable.

2. Protoplasmic Factors

Proper hydration of the protoplasm is essential for photosynthesis. However, isolated chloroplasts are also capable of carrying on photosynthesis under suitable conditions.

3. Accumulation of the End Products of Photosynthesis

Accumulation of carbohydrates in the photosynthesising cells retards the rate of photosynthesis. Quick translocation of the

carbohydrates or the end products of photosynthesis will have a favourable effect on the rate of photosynthesis.

4. Anatomy of Leaf

The rate of photosynthesis is greatly influenced in any leaf or other photosynthesizing part of the plant by the anatomy of that leaf or plant part. The thickness of the cuticle and epidermis, structure and distribution of stomata, distribution and relative proportion of chlorophyllous and non-chlorophyllous mesophyll tissues and structure and distribution of the vascular tissue all influence the rate of photosynthesis.

The effect of the internal structure of the leaves or other photosynthesizing parts of the plant on the rate of the photosynthesis result chiefly due to its influences on the entrance of the CO_2, intensity of light penetrating to chlorophyllous cells, maintenance of the turgidity of such cells and the translocation of the soluble sugars (*i.e.*, the end products of photosynthesis) out of these cells through vascular tissue.

5. Microstructure of chloroplasts

The microstructure of the chloroplasts may also influence the rate of photosynthesis or even determine its course. It is now well known that the plants which show Hatch-Slack pathway contain two types of chloroplasts in contrast to the C_3 plants which have only one type of chloroplasts.

WARBURG'S EFFECT

Despite of the photosynthetic origin of the oxygen, an increase in the O_2 concentration in many plants results in a decrease in the rate of photosynthesis. This phenomenon of the inhibition of photosynthesis by O_2 was first discovered by a German biochemist **Warburg** in 1920 in green alga *Chlorella* and is called as **Warburg's effect**. This effect was subsequently confirmed in wheat by **Mc-Alister** and **Myers (1940)** and is now known to operate in a number of other plants like soybean etc. (C_3 plants). This is not shown by plants like maize, sugarcane, sorghum etc. which are called as C_4 plants.

O_2 causes greatest inhibition of photosynthesis when CO_2 levels are low and light levels are saturating. The inhibition can be relieved by high CO_2 concentrations. Normal atmospheric concentration of O_2 is about 21% which is sufficiently high to slower the rate of photosynthesis that prevails at lower O_2 concentrations in plants showing Warburg's effect (Fig. 64).

Because, the inhibition of th a of photosynthesis is maximum when light levels are saturating it was thought that the O_2 is

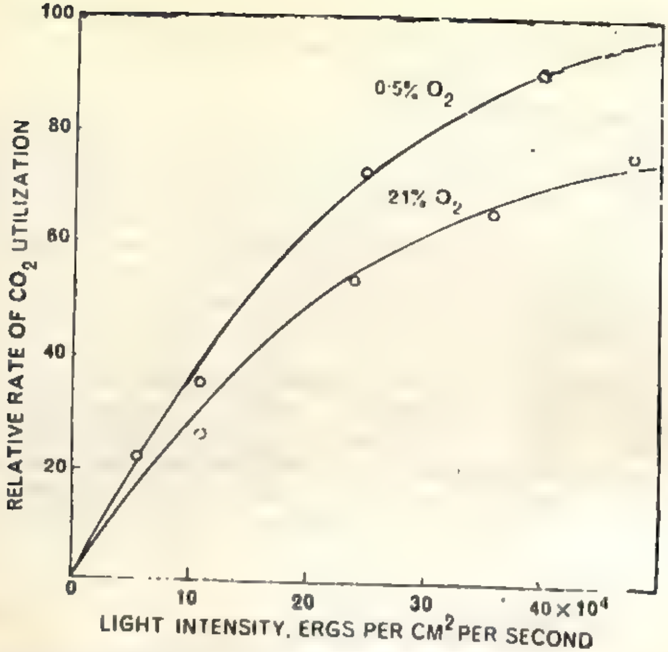

Fig. 64. Relative rates of photosynthesis in wheat at low and high O_2 concentrations under different light intensities. (After Mc Alister & Myers, 1940).

interfering with the generation of reducing power ($NADPH_2$) or as Warburg (1920) suggested the O_2 may be re-oxidising a primary photochemical product and thus competing with CO_2 for reducing power of this product. But the work of **Ellyard & Gibbs (1969)** has shown that generation of reducing power is unaffected by O_2 and that this process would not be rate limiting for most environmental conditions.

There appears to be a close relation between Warburg's effect and the process of **photorespiration** in plants. As will be discussed later, the substrate of photorespiration is **glycolate** which is synthesized from some intermediates of Calvin cycle. In plants which show Warburg's effect increased O_2 concentrations result in **diversion of these intermediates** of **Calvin cycle** into the synthesis of glycolate thereby showing higher rate of photorespiration and consequently **lower photosynthetic productivity**. The plants which do not show Warburg's effect also lack photorespiration and consequently are more efficient photosynthetically.

CARBON DIOXIDE COMPENSATION POINT

This is a common knowledge that the process of photosynthesis takes place in presence of light and CO_2 releasing O_2 during the process while the process of respiration is just its reverse in that it utilises O_2

and releases CO_2. If the light factor is saturating, there will be a certain concentration of CO_2 in the atmosphere at which the rate of photosynthesis will be equal to the rate of respiration or in other words photosynthesis will just compensate for respiration and the value of **apparent photosynthesis** will be zero. This is called as **carbon dioxide compensation point**.

The value of the concentration of CO_2 at the compensation point varies greatly with environmental conditions especially temperature and one plant species to another. For example, some plants like maize, sorghum, sugarcane etc. (*i.e.*, C_4 plants lacking photorespiration) have very low carbon dioxide compensation points (close to 0 ppm). Such plants can deplete almost all of the CO_2 from the surrounding atmosphere at any given O_2 concentration. On the other hand there are certain plants like tomato, wheat, soybean etc. (C_3 plants with photorespiration) which have comparativaly higher CO_2 compensation points (50 ppm or more). In the latter category of plants the CO_2 compensation point increases at higher temperatures probably due to higher photorespiration rate at elevated temperatures.

PHOTORESPIRATION* & GLYCOLATE METABOLISM

(C_2 —CYCLE)

Photorespiration is a special type of respiration shown by many green plants when they are exposed to light. The normal dark respiration (*i.e.* usual mitochondrial respiration) as a rule, is independent of light, its rate being the same in light as well as in dark. The amount of CO_2 released during this process is also equal under both these conditions. But, many workers especially **Krotkov et al** in Canada while working on gaseous exchange of whole green leaves repeatedly noticed that respiratory CO_2 evolution was higher in light than in darkness and that there was a **post-illumination burst of CO_2** output particularly at higher O_2 concentrations. **Krotkov** in 1963 coined the term **photorespiration** to differentiate between these apparently separate forms of CO_2 evolution. Both these types of respiration are also different in sensitivity towards O_2, temperature and metabolic inhibitors and in the specific activity of respiratory substrates following photosynthesis in $C^{14}O_2$.

● Photorespiration is closely related to CO_2 compensation point and usually occurs only in those plants which have comparatively

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* Photorespiration should not be confused with photo-oxidation. While former is a normal process in some green plants the latter is an abnormal and injurious process occurring in extremely intense lights resulting in destruction of cellular components, cells and tissues.

high CO_2 compensation point such as tomato, wheat, oats, green alga *chlorella* etc. (C_3-plants). It is insignificant or rather absent in plants which have very low CO_2 compensation points such as maize, sugarcane etc. (C_4-plants).

● Photorespiration occurs only in chlorophyllous tissues of plants.

● Process of photorespiration is accomplished in 3 different cell organelles viz., **chloroplasts**, **peroxisomes** and **mitochondria**.

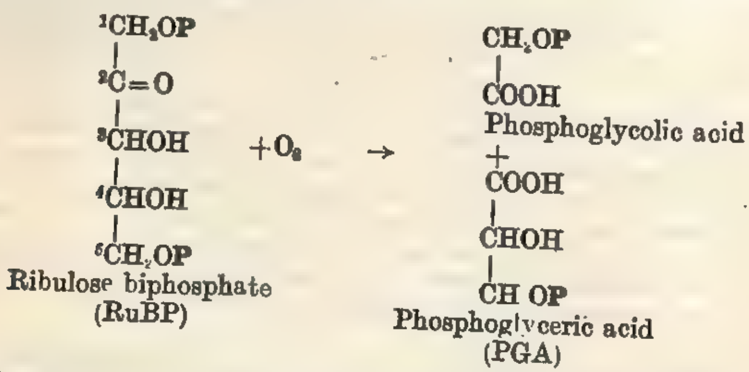
● **Glycolate** (glycolic acid) is the chief metabolite of photorespiration and also its **substrate**. Other important metabolites are the amino acids **glycine** and **serine**.

● Like usual mitochondrial respiration, the photorespiration is also an oxidative process where oxidation of glycolate occurs with subsequent release of CO_2 (post illumination burst of CO_2).

Various steps of the glycolate metabolism (Fig. 65) *i.e.*, synthesis of glycolate and its oxidation with subsequent release of CO_2 (photorespiration) are as follow :

(*i*) Glycolate is synthesized as a side product from some intermediates of photosynthesis in **chloroplasts**. It is probably derived from C_1 and C_2 of the ketose sugar phosphates of the carbon reduction cycle (*i.e.*, Calvin cycle).

It is believed that O_2 competes with CO_2 for the enzyme *Ribulose biphosphate carboxylase** (*RuBP—Carboxylase*). When this enzyme reacts with O_2 instead of CO_2, it is called as *RuBP-oxygenase.* In the latter case, One molecule of phosphoglyceric acid (*PGA*) and one molecule of phosphoglycolic acid are formed from *Ribulose biphosphate*** as shown below :



Phosphoglyceric acid again enters into the Calvin cycle while phosphoglycolic acid is dephosphorylated in the presence of the enzyme *Phosphatase* to form **glycolate**.

* Previously this enzyme was called as *Ribulose diphosphate Carboxylase* (*RuDP-Carboxylase*).

** Previously called as Ribulose diphosphate (RuDP).

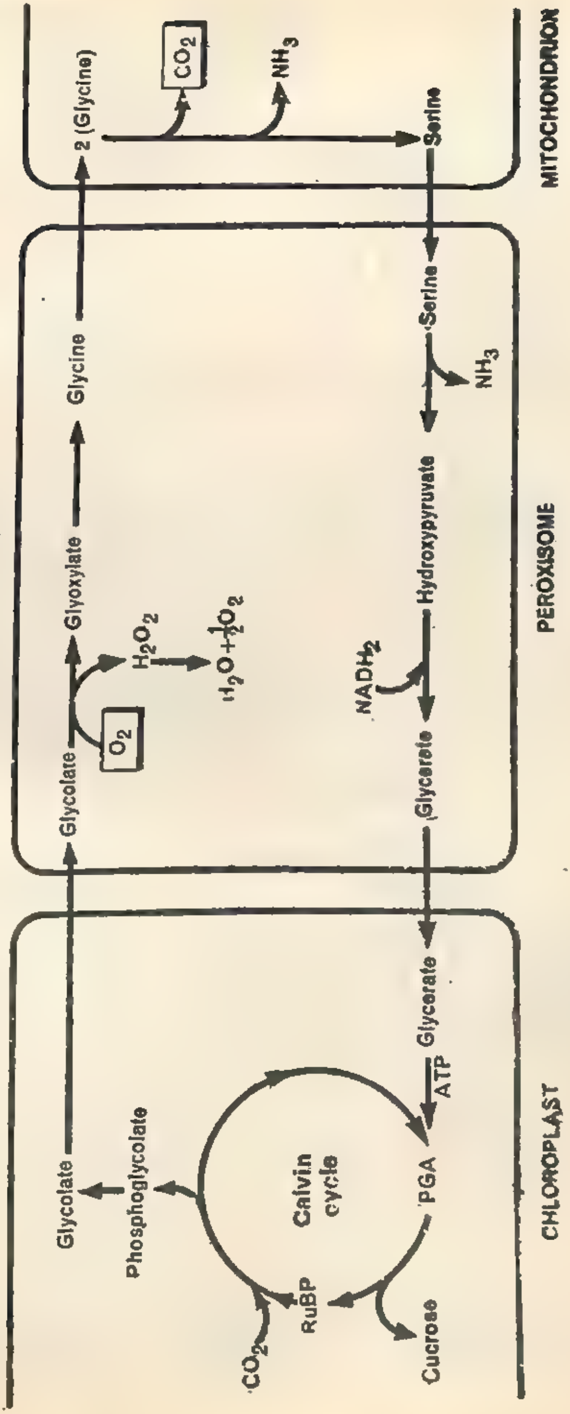


Fig. 65. Glycolate metabolism during photorespiration. (See text for details).

$$\underset{\text{Phosphoglycolic acid}}{\begin{array}{l} CH_2OP \\ | \\ COOH \end{array}} \xrightarrow[H_2O]{\textit{Phosphatase}} \underset{\text{Glycolate}}{\begin{array}{l} CH_2OH \\ | \\ COOH \end{array}} + P\,(OH)$$

(*ii*) From chloroplasts, the glycolate migrates into *peroxisome* where it is oxidised (Photorespired) to *glyoxylate* in the presence of the enzyme *glycolic acid oxidase*

$$\underset{\text{Glycolate}}{\begin{array}{l} CH_2OH \\ | \\ COOH \end{array}} + O_2 \longrightarrow \underset{\text{Glyoxylate}}{\begin{array}{l} CHO \\ | \\ COOH \end{array}} + H_2O_2$$

The hydrogen peroxide formed is removed by the enzyme *catalase.*

$$H_2O_2 \rightarrow H_2O + \tfrac{1}{2}\,O_2$$

(*iii*) Glyoxylate is now converted into an amino acid **glycine.** This is a transamination reaction which takes place at the expense of L-Glutamate and in the presence of the enzyme *L-Glutamate glyoxylate transaminase.*

$$\underset{\text{Glyoxylate}}{\begin{array}{l} CHO \\ | \\ COOH \end{array}} + \underset{\text{L-Glutamate}}{\begin{array}{l} COOH \\ | \\ CH_2 \\ | \\ CH_2 \\ | \\ CHNH_2 \\ | \\ COOH \end{array}} \longrightarrow \underset{\text{Glycine}}{\begin{array}{l} CH_2NH_2 \\ | \\ COOH \end{array}} + \underset{\alpha\text{-ketoglutaric acid}}{\begin{array}{l} COOH \\ | \\ CH_2 \\ | \\ CH_2 \\ | \\ C{=}O \\ | \\ COOH \end{array}}$$

(*iv*) The glycine formed in peroxisomes migrates into **mitochondria** where 2 molecules of glycine react to form one molecule of another amino acid **Serine** with liberation of $\mathbf{CO_2}$ (post-illumination burst of CO_2 & photorespiration) and also NH_3. This reaction is catalysed by the enzyme *serine hydroxymethyl transferase.*

$$2\,\underset{\text{Glycine}}{\begin{array}{l} CH_2NH_2 \\ | \\ COOH \end{array}} + \tfrac{1}{2}\,O_2 \longrightarrow \underset{\text{Serine}}{\begin{array}{l} CH_2OH \\ | \\ CHNH_2 \\ | \\ COOH \end{array}} + \mathbf{CO_2} + NH_3$$

(*v*) Serine so formed is apparently recycled back into the pool of photosynthetic intermediates of calvin cycle in chloroplasts. This is probably mediated by the formation of **hydroxypyruvate** and **glyceric acid**. Glyceric acid on phosphorylation with ATP can be

converted into phosphoglyceric acid (PGA). The latter is well known intermediate of Calvin cycle. This series of reactions can be summarised as follows :

$$\underset{\text{Serine}}{\begin{array}{l} CH_2OH \\ | \\ CHNH_2 \\ \\ COOH \end{array}} \xrightarrow[\searrow NH_3]{} \underset{\text{Hydroxypyruvate}}{\begin{array}{l} CH_2OH \\ | \\ C{=}O \\ | \\ COOH \end{array}}$$

$$\underset{\text{Hydroxypyruvate}}{\begin{array}{l} CH_2OH \\ | \\ C{=}O \\ | \\ COOH \end{array}} \xrightarrow[NADH_2 \nearrow\searrow NAD]{} \underset{\text{Glyceric acid}}{\begin{array}{l} CH_2OH \\ | \\ CHOH \\ | \\ COOH \end{array}}$$

$$\underset{\text{Glyceric acid}}{\begin{array}{l} CH_2OH \\ | \\ CHOH \\ | \\ COOH \end{array}} \xrightarrow[ATP \nearrow\searrow ADP]{} \underset{\text{Phosphoglyceric acid (PGA)}}{\begin{array}{l} CH_2OP \\ | \\ CHOH \\ | \\ COOH \end{array}}$$

Thus, starting from intermediates of Calvin cycle with the synthesis of glycolate, serine is formed which again is converted into intermediates of calvin cycle thus completing the **glycolate cycle**. And because glycolate and some other metabolites of this cycle *e.g.*, glyoxylate and glycine are **2-C compounds**, the glycolate metabolism or glycolate cycle is also called as **C_2 —cycle**.

Factors affecting photorespiration

As described earlier photorespiration is closely associated with CO_2 compensation point. Besides the particular plant species* (C_3 or C_4 plant), the factors which influence CO_2 compensation point also affect rate of photorespiration. Thus, rate of photorespiration is higher when CO_2 concentration is higher and O_2 concentration is low. Higher temperatures also have a favourable effect on this process. On the other hand inhibitors of *glycolic acid oxidase* such as α-**hydroxysulphonates** inhibit the process of photorespiration.

Significance of photorespiration

Positive function of photorespiration in plants is not yet known. It rather seems to be a doubly wasteful process. Firstly, it has been estimated that during photosynthesis by algae and C_3 plants up to

* Although peroxisomes were found in all leaf homogenates tested, but the photorespiratory enzymes were especially low in C_4 plants (Tolbert et al. 1969). This explains very little or no photorespiration in C_4 plants.

50% of the CO_2 fixed may have to pass through photorespiratory process (glocolate pathway) to form carbohydrates such as sucrose thereby resulting in considerable decrease of photosynthetic productivity. Secondly, unlike usual mitochondrial respiration neither reduced co-enzymes are generated in photorespiration nor the oxidation of glycolate is coupled with the formation of ATP molecules. According to Hatch & Slack (1970) photorespiration is a **metabolic adjunct** to the Calvin cycle (*i.e.*, it has been added to the Calvin cycle but essentially is not its part).

However, the knowledge about the process of photorespiration is of great importance to Agriculturists. By manipulating the different atmospheric conditions, use of inhibitors of glycolic acid oxidase such as α-hydroxysulphonates, and through genetic control, the process of photorespiration can be regulated and consequently the **photosynthetic productivity** can be increased manifold.

CHEMOSYNTHESIS

There are certain **aerobic bacteria** which do not have chlorophyll but can manufacture organic food from CO_2 and H_2O. For this, instead of utilising light energy they make use of the **chemical energy** which is evolved during the **oxidation of some inorganic substances** by them. This process of the manufacture of the organic food matter by bacteria making use of the chemical energy is called as **chemosynthesis**. Some of the common examples of chemosynthetic bacteria are given below :

(i) Nitrifying Bacteria

Nitrosomonas and *Nitrosococcus* oxidise ammonia to nitrite and chemical energy is released.

$$2NH_3 + 3O_2 \rightarrow 2HNO_2 + 2H_2O + \text{Chemical Energy}$$

Nitrobacter oxidises nitrite to nitrate to release chemical energy which is then utilised in the manufacture of the food,

$$2HNO_2 + O_2 \rightarrow 2HNO_3 + \text{Chemical energy}$$

(ii) Sulphur Bacteria

Beggiatoa and *Thiothrix* oxidise hydrogen sulphide to sulphur and release sufficient amount of chemical energy for subsequent food synthesis

$$2H_2S + O_2 \rightarrow 2H_2O + \text{Chemical energy.}$$

(iii) Iron Bacteria

Ferrobacillus, Leptothrix etc., oxidise ferrous iron to ferric iron and release chemical energy.

$$4FeCO_3 + O_2 + 6H_2O \rightarrow 4Fe\,(OH)_3 + 4CO_2 + \text{Chemical energy.}$$

(iv) Carbon Bacteria (*e.g., Bacillus oligocarbophilus*)

$$2CO + O_2 \rightarrow 2CO_2 - \text{Chemical energy.}$$

(v) Hydrogen Bacteria (*e.g., Bacillus pantotrophus*)

$$2H_2 + O_2 \rightarrow 2H_2O + \text{Chemical Energy.}$$

CARBON CYCLE IN NATURE

All the carbon in plants is derived from the CO_2 of the atomsphere where it constitutes about 0·03% by volume of the latter. Green plants consume CO_2 of the atmosphere during photosynthesis in order to manufacture their food and release it again into the atmosphere either during respiration or indirectly through other means. Therefore, the equilibrium of CO_2 is maintained in the atmosphere due to the operation of a **carbon cycle in nature.** Various steps of the carbon cycle in nature which is also shown in Fig. 66 , are as follow :

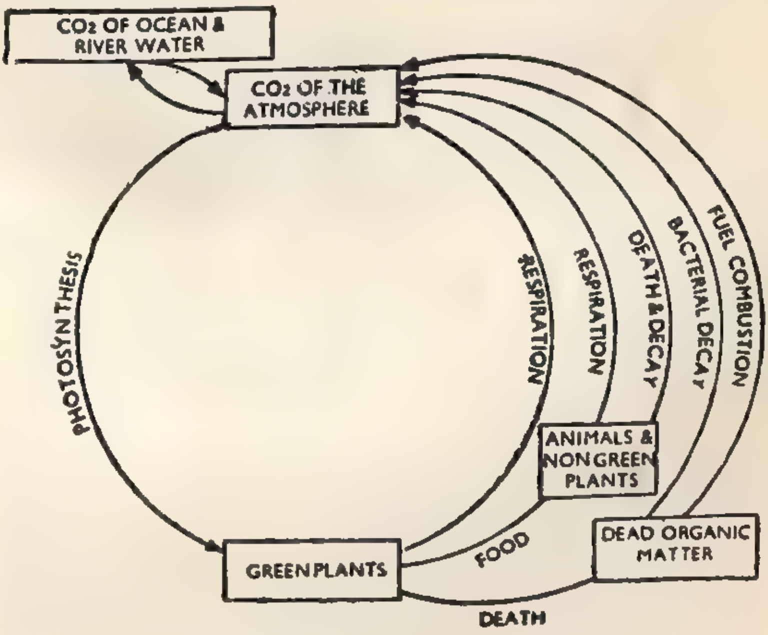


Fig. 66. Carbon cycle in nature.

(*i*) CO_2 of the atmosphere is consumed by green plants and to some extent by chemosynthetic bacteria for the manufacture of their food.

(*ii*) When green plants respire CO_2 is released into the atmosphere.

(*iii*) Bacterial decay of the dead organic matter after the death of green plants results in liberation of CO_2 which goes into the atmosphere.

(*iv*) Dead organic matter of the green plants is widely used as fuel in the form of wood, coal, oil etc., which on combustion release CO_2 into the atmosphere.

(*v*) Animals and non-green plants derive their food ultimately from green plants. They also release CO_2 during respiration.

(*vi*) Bacterial decay of the dead animals and non-green plants also results in the liberation of CO_2 into the atmosphere.

(*vii*) Whenever the equilibrium of CO_2 in the atmosphere is disturbed, CO_2 of ocean and river water goes into the atmosphere or *vice versa*.

CRASSULACEAN ACID METABOLISM (CAM) AND DARK CO_2 FIXATION

Under natural conditions the acidity of green shoots of some non-halophytic succulents and semi-succulent plants increases at night and decreases during the following day. This diurnal change in acidity was first discovered in a Crassulacean plant *Bryophyllum calycinum* and hence, has been termed as **Crassulacean acid metabolism** (**CAM**). Crassulacean acid metabolism occurs only in **green organs** and the plants which exhibit it belong to a number of different families. It is especially noticeable in leaves of *Bryophyllum*, *Kalanchoe*, *Sedum*, *Kleinia*, *Crassula* and fleshy green stems of *Opuntia*.

The distinctive diurnal fluctuation in acidity in plants showing CAM is predominantly due to changes in amounts of **Vacuolar malic acid**. During night malic acid is synthesized utilising CO_2 (dark CO_2 fixation) which then accumulates in the vacuole and may account for about 85% of the total titrable acid content. During the following day this malic acid is consumed (oxidised to release CO_2) resulting in decrease of acidity. Besides malic acid, some other acids like citric acid and iso-citric acid also contribute to the total titrable acidity but their amount is negligible and moreover these do not show consistent diurnal pattern of fluctuation as exhibited by malic acid.

Diurnal changes in gaseous exchanges during CAM.

During the dark synthesis of malate in CAM (resulting in the acidification), oxygen is absorbed continuously but, in the early

stages, little or no CO_2 is evolved. This results in a **respiratory quotient** (**R.Q.**)* of very low or even zero and sometimes a negative value.

When the accumulation of malate is complete, the CO_2 is evolved rapidly and the **R.Q.** is unity.

During light deacidification, O_2 is continuously evolved but initially the absorption of CO_2 is very slow. This results in high values of **photosynthetic quotient** (ml. O_2 evolved/ml. CO_2 uptake). However, as the deacidification slows down, the uptake of CO_2 increases rapidly until deacidification is complete. In successive light periods, the vol. of CO_2 uptake equals to the vol. of O_2 given out and hence, the photosynthetic quotient falls to unity.

Factors influencing diurnal fluctuations in acidity

The amplitude of the diurnal fluctuations in acidity varies with growth conditions and age of the plant. It increases with unfolding of the leaves until they are fully expanded and decreases when they enter senescence. Apart from these, the seasonal changes also have profound effect on it through changes in day and night temperatures, photosynthetic activity and at least in some plants in the length of the day.

Synthesis of malate during night or dark CO_2 fixation

Large amounts of starch are consumed during acidification which indicates that carbohydrates are the source of malate synthesis, the overall process being represented by the following equation :

$$C_6H_{12}O_6 + 2CO_2 \rightarrow \underset{\text{Malate}}{2C_4H_6O_5}$$

It is now generelly believed that the malate is synthesised during night in reactions in which some product derived from carbohydrate reserves *e.g.*, **pyruvate** or most likely **phosphoenol pyruvate** (**PEP**) is **carboxylated** to produce malate either directly or first forming **oxaloacetic acid** which is then reduced to malate according to the following reactions :—

1. $\text{Pyruvate} + CO_2 + NADPH_2 \xrightleftharpoons{\text{Malic enzyme}} \text{Malate} + NADP$

2. $PEP + CO_2 + ADP \xrightleftharpoons{\text{PEP—Carboxykinase}} \text{Oxaloacetate} + ATP$

3. $PEP + CO_2 + H_2O \xrightarrow{\text{PEP—carboxylase}} \text{Oxaloacetate} + Pi$

4. $\text{Oxaloacetate} + NADH_2 \xrightleftharpoons{\text{Malate dehydrogenase}} \text{Malate} + NAD$

* R.Q. = Vol. of CO_2 given out/vol. of O_2 taken in. For details see chapter 16.

Experiments with ^{14}C—labelled $^{14}CO_2$ uptake in dark have shown constant distribution of radioactivity in the ratio of 1 : 2 in C—1 and C—4 of malate respectively. This has led to the present hypothesis that the PEP utilised in synthesis of malate arises not from carbohydrate breakdown but from **3—phosphoglyceric acid (3—PGA)** produced from **ribulose diphosphate (RuDP)** as in photosynthesis by the action of *Ribulose diphosphate carboxylase.* Various postulated steps of this hypothesis involving 2-sequential CO_2 fixations are given in Fig. 67.

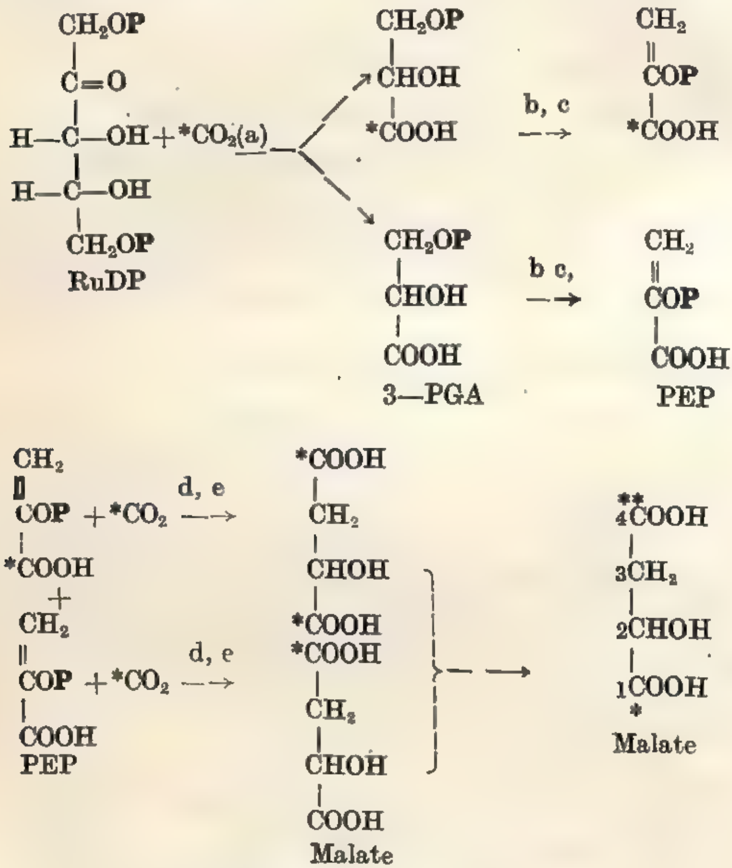


Fig. 67. Postulated steps in malate synthesis in CAM. Note 2/3 distribution of radioactivity (*) in C—4 and 1/3 in C—1 of malate (a, RuDP—Carboxylase ; b, phosphogly ceromutase ; c, enolase ; d, PEP—carboxylase ; e, malate dehydrogenase).

(Malate may also be formed through glyoxylate cycle. But this possibility is completely ruled out in plant organs showing CAM because glyoxylate cycle does not operate in such organs. It functions significantly only in germinating fatty seeds. For details of glyoxylate cycle see chapter 14)

Consumption of malate in dark deacidification

After the plant organs showing CAM are fully acidified and if they remain in dark, deacidification of malate occurs with the liberation of CO_2. The CO_2 thus released is superimposed upon the respiratory exchange of O_2 & CO_2 and results in high values of R.Qs. These may sometime exceed the value of even 1·33 which is the maximum value of R.Q. if malate consumed is fully oxidised to CO_2+H_2O :—

$$\underset{\text{Malate}}{C_4H_6O_5}+3O_2 \longrightarrow 4CO_2+3H_2O$$

$$R.Q. = \frac{4}{3} = 1{\cdot}33$$

Previously, there we̍re some indications that during dark deacidification some carbohydrate accumulation may occur. There is, however, no experimental evidence to show that matate is converted into carbohydrates to any appreciable extent in periods of the dark deacidification under normal circumstances.

Consumption of malate in light deacidification

When acidified organs are exposed to light in air, rapid consumption of malate occurs resulting in **deacidification** (due to CO_2 release from malate). The carbon of the malate is incorporated into carbohydrate. Previously it was thought that the malate in light was first decarboxylated to release CO_2 and the remaining C_3 fragments were directly converted into carbohydrate (Malate is a 4—C compound). But, experiments by various investigators especially **Moyse et al** in France, have clearly shown that as in dark deacidification, the malate in light is also completely oxidised to CO_2 and water. The CO_2 thus produced is then consumed in normal photosynthetic reaction sequence to yield carbohydrates. **Moyse et al** (1957) have also suggested that the faster utilisation (oxidation) of malate in light than in dark may be due to the liberation of O_2 in photosynthesis in light and this O_2 enhancing the oxidative activity of the cytoplasm of green organs in which CAM is taking place.

(The enzymes which are involved in the malate synthesis during CAM are not confined only to those plants in which CAM occurs but have wide occurrence in other plants too. It is not known why CAM occurs only in certain plants and not in others. It has been suggested that (1) probably in the cells of plants showing CAM, the enzymes are associated in some special way or distributed differently than those in other plants, (2) the CAM is the natural consequence of some yet unknown reaction occurring only in some succulent and semi-succulent plants (3) the most attractvie hypothesis is that the cells showing CAM have unique power for regulating the transport of malate within the cells from cytoplasm into the vacuole and *vice versa*).

10

Translocation of Organic Solutes

The movement of organic food materials or the solutes in soluble form from one place to another in higher plants is called as **translocation of organic solutes**.

Translocation of organic solutes is essential in higher plants because :—

(*i*) In higher plants, only the green parts can manufacture food and it must be supplied to other non-green parts for consumption and also for storage.

(*ii*) During the germination of the seeds, the insoluble reserve food material of the seed is converted into soluble form and is supplied to the growing regions of the young seeding till it has developed its own photosynthetic system *i.e.*, leaves.

Translocation of organic solutes always takes place from the region of higher concentration of soluble form *i.e.*, the **supply end** to the region of lower concentration of its **soluble form** *i.e.*, the **consumption end**.

DIRECTIONS OF TRANSLOCATION

Translocation of organic solutes may take place in the following directions :—

1. Downward Translocation.

Mostly, the organic food material is manufactured by leaves and is translocated downward to stem and the roots for consumption and storage.

2. Upward Translocation

It takes place mainly during the germination of seeds, tubers etc. when stored food after being converted into soluble form is

supplied to the upper growing parts of the young seeding till it has developed green leaves.

Upward translocation of solutes also takes p'ace through stem (i) to buds which resume growth in the spring (ii) to developing leaves situated closer to its apex (iii) to opening flowers and developing fruits which are situated near the ends of the branches.

3. Radial Translocation

Radial translocation of organic solutes also takes place in plants from the cells of the pith to cortex.

PATH OF THE TRANSLOCATION OF ORGANIC SOLUTES

1. Path of Downward Translocation

Downward translocation of the organic solutes takes place through **Phloem**. This view is supported by the following evidences: —

(i) **Tissues other than phloem cannot account for downward translocation**. Ascent of sap takes place through xylem, so naturally organic solutes are not translocated through it. The cells of the ground tissue are structurally neither suitable for translocation nor they contain soluble organic solutes which could be translocated. These cells usually have organic solutes in insoluble form.

Thus only phloem is left which can account for translocation of the organic solutes. The end to end arrangement of the sieve tubes in phloem whose cross walls are perforated by sieve pores form continuous channels and is best suited for it. Further, in Cucurbits where the leaves are usually larger, the stem contains **bicollateral** vascular bundles to cope with the rapid translocation of food materials through it.

(ii) **Blocking of phloem**. Translocation of food materials stops when sieve pores are plugged due to the deposition of a chemical compound, the callose.

(iii) **Chemical analysis of phloem sap**. Cells of phloem contain large quantities of organic solutes in soluble form.

(iv) **Isotopic studies**. It has been observed that if a leaf of the plant is allowed to photosynthesize in presence of labelled $C^{13}O_2$ the translocation of carbohydrates labelled with C^{13} isotope takes place through the stem. But, if some segments of the stem including phloem were killed by hot wax no movement of carbohydrates could be detected.

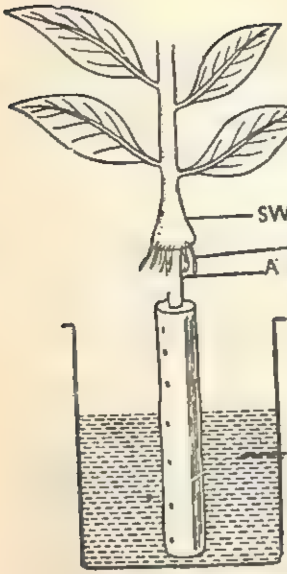


Fig. 68. Ringing experiment.

(v) Ringing experiment. If a ring of bark including phloem is removed from the stem of a plant, the downward translocation of food material stops and food material accumulates just above the ring. As a result after sometime, the tissue above the ring swells and may even develop adv. roots (Fig. 68) while the lower parts of the plant below the ringed portion gradually dry up.

2. Path of upward Translocation

There has been controversy regarding the path of upward translocation of organic solutes in plants. Although translocation of organic solutes takes place through phloem, but under certain conditions it may take place through xylem.

3. Path of Radial Translocation

Radial translocation of organic solutes from pith to cortex takes place through medullary rays.

MECHANISM OF TRANSLOCATION THROUGH PHLOEM

Various theories have been put forward to explain the mechanism of phloem conduction but they are not fully satisfactory. Among them **Munch's** (1930) hypothesis is most convincing.

MUNCH'S MASS FLOW OR PRESSURE FLOW HYPOTHESIS

According to this hypothesis put forward by **Munch** (1930) and elaborated by **Crafts** (1938) and others, the translocation of organic solutes takes place **en mass** through phloem along a gradient of turgor pressure from the region of higher conc. of soluble solutes *i.e.*, supply end to the region of lower conc. *i.e.*, consumption end.

The principle involved in this hypothesis can be explained by a simple physical system as shown in the Fig. 69.

Two membranes **X** and **Y** permeable only to water and dipping in water are connected by a tube **T** to form a closed system. Membrane **X** contains more concentrated sugar solution than in membrane **Y**.

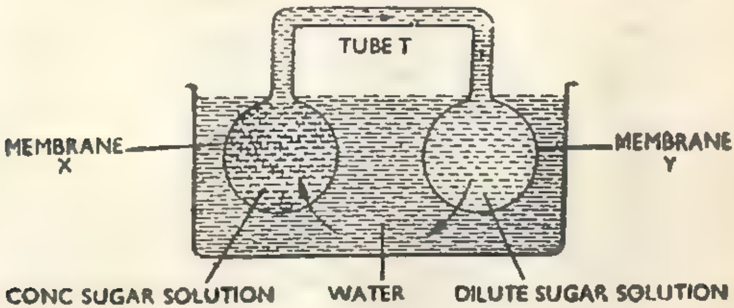


Fig. 69. Diagram illustrating the principle of Munch Mass Flow hypothesis.

Due to higher osmotic pressure of the concentrated sugar solution in membrane **X**, water enters into it so that its **turgor pressure** is increased. The increase in the turgor pressure results in **mass flow** of sugar solution to membrane **Y** through the tube **T** till the concentration of sugar solution in both the membranes is equal.

If in the above system it could be possible to maintain continuous supply of sugars in membrane **X** and its utilization or conversion into insoluble form in membrane **Y**, the flow of sugar solution from **X** to **Y** will continue indefinitely.

According to Munch's hypothesis a similar analogous system for the translocation of organic solutes exists in plants. As a result of photosynthesis, the **mesophyll cells** in the leaves contain higher concentration of organic food material in them in soluble form and correspond to membrane **X** or supply end. The cells of **stem** and **roots** where the food material is utilized or converted into insoluble form correspond to membrane **Y** or consumption end. While the **sieve tubes** in phloem which are placed end to end correspond to the tube **T**.

Mesophyll cells draw water from the xylem of the leaf due to higher osmotic pressure and suction pressure of their sap so that their turgor pressure is increased. The turgor pressure in the cells of stem and the roots is comparatively low and hence, the soluble organic solutes begin to flow **en mass** from mesophyll through phloem down to the cells of stem and the roots under the **gradient of turgor pressure**. In the cells of stem and the roots the organic

solutes are either consumed or converted into insoluble form and the **excess water is released into xylem** through cambium (Fig. 70).

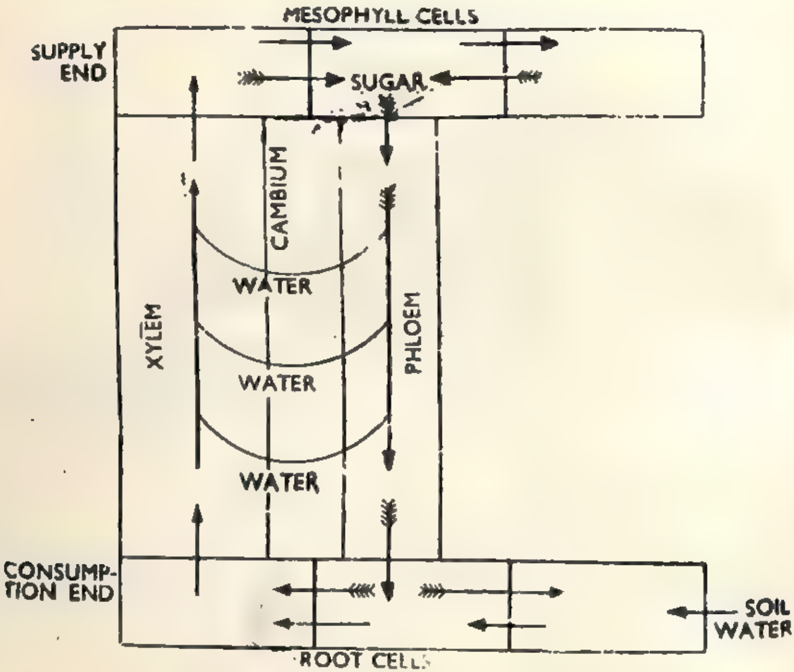


Fig. 70. Diagram to illustrate the mechanism of solute translocation according to the Munch hypothesis.

Demerits of Munch Hypothesis

(1) This hypothesis accounts for the translocation in only one direction at a time, although there may be simultaneous upward and downward translocation of solutes.

(2) There is considerable doubt regarding the magnitude of the turgor pressure at the supply end which may not be sufficient enough to overcome the resistance offered by the sieve plates in the translocation of solutes through sieve tubes.

(3) Turgor pressure may not always be higher at the supply end.

(4) This hypothesis is based on purely physical assumptions and does not take into account the fact that whole of the translocation process is dependent upon the plant's metabolism and the metabolic energy.

OTHER THEORIES OF MECHANISM OF TRANSLOCATION

(1) PROTOPLASMIC STREAMING THEORY

According to this hypothesis first proposed by **De Vries** (1885) and later supported by **Curtis** (1935) protoplasmic streaming occurs in sieve tube elements of phloem and the solute molecules caught up in the circulating cytoplasm are carried from one end to the other end of the sieve tube from where they diffuse to the next sieve tube elements through the cytoplasmic strands in the sieve plates.

This theory was supported because (i) it accounted for simultaneous movement of solutes in both upward and downward directions in the same sieve tube and (ii) that the factors like low temperature and oxygen deficiency which retard protoplasmic streaming also checked the translocation of solutes.

But, the strongest objection against this theory is that the protoplasmic streaming has not been observed in mature sieve tube elements.

Protoplasmic theory has recently been re-emphasized by **Cany** (1952) and **Thaine** (1962, 64) who observed the '**transcellular' strands** (cytoplasmic strands) traversing the sieve tube elements in petiolar tissue. They also observed (i) the movement of solute particles from one sieve tube element to another and (ii) particles moving in opposite directions in adjacent transcellular strands in the same sieve tube element.

(2) INTERFACIAL FLOW HYPOTHESIS

According to this hypothesis proposed by **Van den Honert** (1932) the solute particles could move along the interfaces such as between the vacuole and the protoplast. But this theory did not find support, the main objections against this theory being (i) the lack of evidences in support of such a mechanism in plants and (ii) that the plant membranes are not static but constantly changing.

(3) ACTIVATED DIFFUSION HYPOTHESIS

According to this hypothesis put forward by **Mason** and **Phillis** (1936) the protoplasm of the sieve tube elements in some way hastens the diffusion of the solutes probably (i) by activating the diffusing molecules or (ii) by decreasing the resistance of the protoplasm to their diffusion. Although they could think of the participation of the respiratory energy during this process but were unable to give details of such a mechanism, and hence, this theory also has not been accepted.

(4) ELECTRO-OSMOTIC THEORY

According to this theory put forward by **Fensom** (1957) and **Spanner** (1958) the translocation of solutes through sieve tubes takes place probably due to an electric potential across the sieve

plates. The electric-potential could be maintained by the circulation of K^+ at the sieve plates.

But, due to lack of evidences this theory could not be elaborated further.

11

Respiration

RESPIRATION

The energy stored in carbohydrate molecules during photosynthesis is released during **cellular oxidation** of carbohydrates into CO_2 and H_2O. This is called as **Respiration**. In respiration the oxidation of various organic food substances like carbohydrates, fats, proteins etc., may take place. Among these **glucose** is commonest. Its oxidation proceeds as is shown in the following equation :—

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{Energy (686 K. Cal)}.$$

This oxidation is not so simple and does not take place in one step. Breakdown of glucose involves many steps releasing energy in the form of **ATP** molecules and forming a number of carbon compounds (**Intermediates**) in a very well organised sequence.

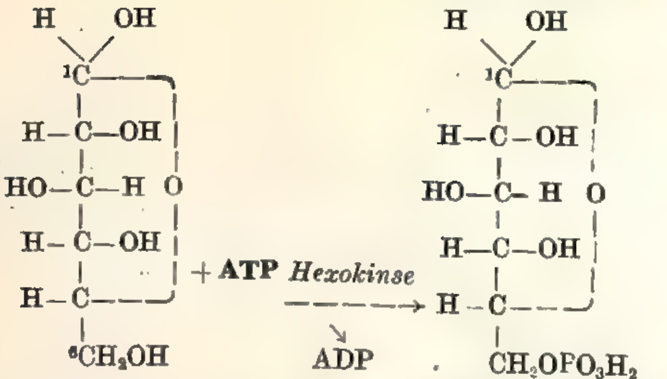
MECHANISM OF RESPIRATION

It can be studied under the following heads :—

(A) GLYCOLYSIS (EMBDEN-MEYERHOF-PARANAS-PATHWAY)

In glycolysis which can take place even in the absence of O_2, 6-carbon compound glucose (**hexose**) is broken down through a series of reversible enzymic reactions into 3-carbon compound, the **pyruvic acid (a triose)**. Various steps of glycolysis are as follow :—

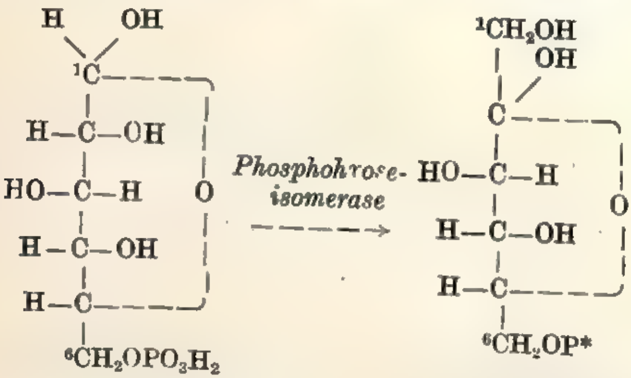
(1) Glucose molecule reacts with **ATP** molecule in the presence of the enzyme *hexokinase* to form **glucose-6-phosphate (Robinson's ester)**.



Glucose

Glucose-6 Phosphate (Robinson's ester)

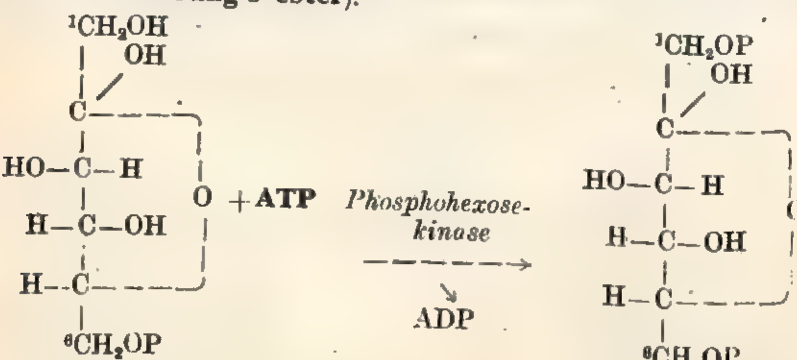
(2) Glucose 6-Phosphate is isomerised into **Fructose 6-Phosphate (Newberg's ester) in the presence of** *phospohexose isomerase.*



Glucose-6-Phosphate

Fructose-6-Phosphate (Newberg's ester)

(3) Fructose 6-Phosphate reacts with one mol. of **ATP** in the presence of *phosphohexose kinase* froming **Fructose 1, 6-diphosphate (Harden and Young's ester)**.



Fructose-6-Phosphate

Fructose 1, 6-Diphosphate (Harden & Young's ester)

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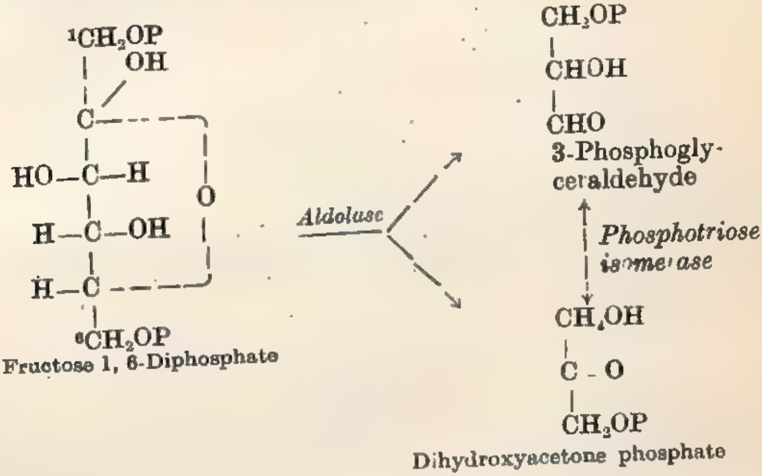
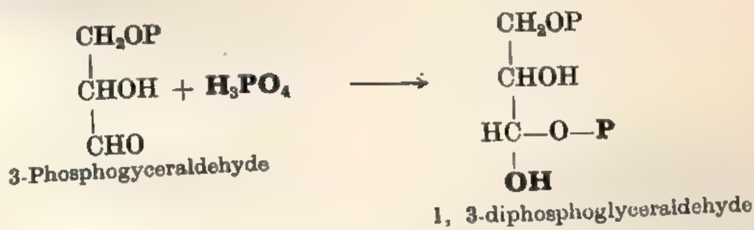
* $P = PO_3H_2$

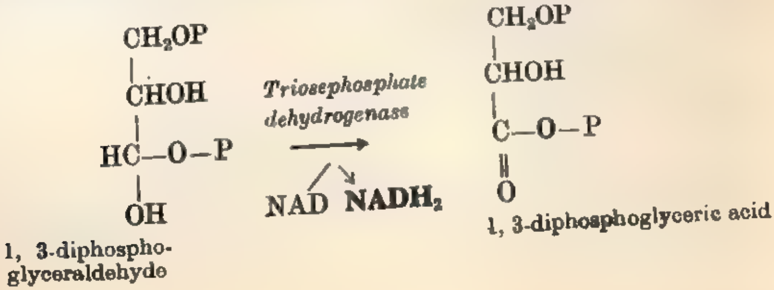
(4) Fructose 1,6—Diphosphate is converted into two **trioses 3-Phosphoglyceraldehyde** and **Dihydroxy acetone phosphate** in the presence of *Aldolase*. The two trioses may isomerise into each other in the presence of *phosphotriose isomerase*.



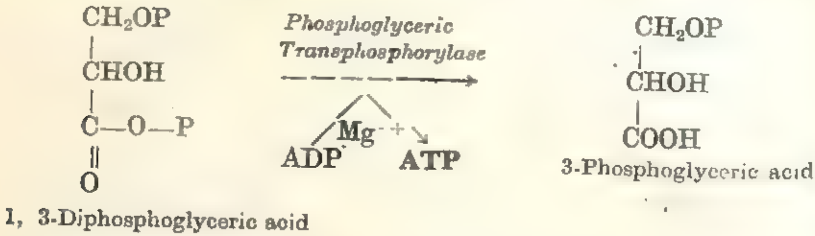
(5) 3-phosphoglyceraldehyde reacts with H_3PO_4 and forms **1, 3-diphosphoglyceraldehyde**. The reaction is non-enzymatic.



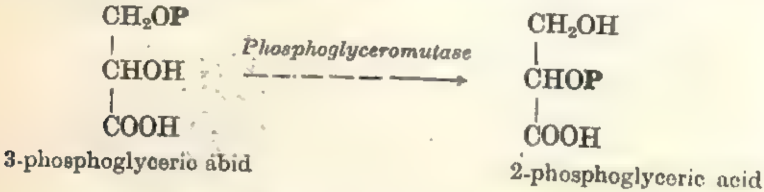
(6) 1, 3-diphosphoglyceraldehyde, in presence of *Triose phosphate dehydrogenase* and coezyme NAD, is oxidised to form **1, 3-diphosphoglyceric acid**. **NAD is reduced**. This reaction is inhibited by M/1000 conc. of Iodoacetate.



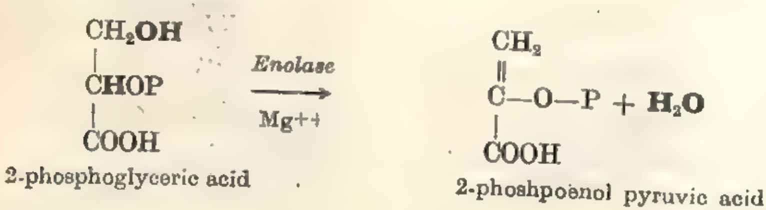
(7) 1, 3-Diphosphoglyceric acid reacts with ADP in presence of *phosphoglyceric transphosphorylase* to form one mol. of **ATP** and **3-Phosphoglyceric acid**.



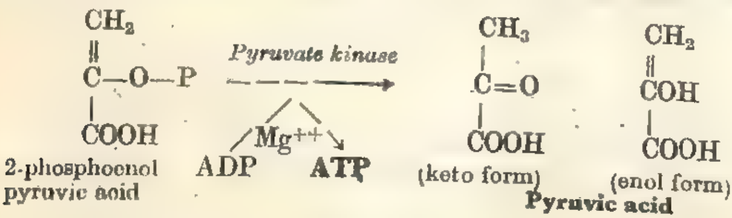
(8) 3-Phosphoglyceric acid is isomerised into **2-Phosphoglyceric acid** in presence of enzyme *Phosphoglyceromutase.*



(9) 2-Phosphoglyceric acid is converted into **2-Phosphoenol pyruvic acid** in presence of *Enolase.* The reaction is inhibited by M/40 conc. of NaF.



(10) 2-Phosphoenol pyruvic acid reacts with ADP to form one molecule of **ATP** and **Pyruvic acid**. The enzyme *pyruvate kinase* catalyses this reaction.



The carboxylic group of the pyruvic acid is derived from carbon no. 3 or 4 of the glucose molecule.

Glucose

$\updownarrow$ $+ATP$ *Hexokinase*

Glucose-6-Phosphate (Robinson's ester)

$\updownarrow$ *Phosphohexose isomerase*

Fructose-6-Phosphate (Newberg's ester)

$\updownarrow$ $+ATP$ *Phosphohexokinase*

Fructose 1, 6-diphosphate (Harden and Young's ester)

$\updownarrow$ Aldolase

3-Phosphoglyceraldehyde $\xleftrightarrow{\textit{Phosphotriose-isomerase}}$ Dihydroxyacetone phosphate

$\updownarrow$ $+ H_3PO_4$

1, 3-diphosphoglyceraldehyde

$\updownarrow$ *Triosephosphate-dehydrogenase* (NAD $\rightarrow$ $NADH_2$)

1, 3 diphosphoglyceric acid

$\updownarrow$ *Phosphoglyceric-transphosphorylase* (ADP $\xrightarrow{Mg^{++}}$ ATP)

(All the enzymes of glycolysis are found in cytoplasm in soluble form.)

3-Phosphoglyceric acid

$\updownarrow$ *Phosphoglyceromutase*

2-Phosphoglyceric acid

$\updownarrow$ Mg^{++} *Enolase* $-H_2O$

2-Phosphoenol pyruvic acid

$\updownarrow$ *Pyruvate kinase* (ADP $\xrightarrow{Mg^{++}}$ ATP)

Pyruvic acid

Fig. 71 . Glycolysis (EMP-Pathway)

(B) ANAEROBIC-RESPIRATION (FERMENTATION)

In the absence of molecular oxygen, pyruvic acid undergoes **anaerobic respiration** or **fermentation**. Two types are common :

(a) Alcoholic Fermentation

The Pyruvic acid is first decarboxylated to acetaldehyde in the presence of *carboxylase.* Thiamine pyro-phosphaste (TPP) is required as co-factor.

$$\underset{\text{Pyruvic acid}}{2CH_3CO{\cdot}COOH} \xrightarrow[\text{TPP}]{\textit{Carboxylase}} \underset{\text{Acetaldehyde}}{2CH_3CHO} + 2CO_2$$

Acetaldehyde is then reduced to ethyl alcohol by the enzyme *alcohol dehydrogenase.* Coenzyme **$NADH_2$** is oxidised.

$$\underset{\text{Acetaldehyde}}{CH_3CHO} + \underset{\text{Reduced}}{NADH_2} \xrightarrow{\textit{Alc. dehydrogenase}} \underset{\text{Ethyl alcohol}}{CH_3CH_2OH} + \underset{\text{Oxi.}}{NAD}$$

(b) Lactic Acid Fermentation

Here the pyruvic acid is converted into **Lactic acid** by the enzyme *Lactic-dehydrogenase.* Coenzyme **$NADH_2$** is oxidised.

$$\underset{\text{Pyruvic acid}}{CH_3CO{\cdot}COOH} + NADH_2 \xrightarrow{\textit{Lactic-dehydrogenase}} \underset{\text{Lactic acid}}{CH_3CHOHCOOH} + NAD$$

(C) AEROBIC RESPIRATION—THE KREB'S CYCLE

If the molecular oxygen is available **aerobic respiration** takes place and the pyruvic acid produced in glycolysis enters into **Kreb's cycle** for further oxidation. Kreb's cycle is also known as **Citric Acid Cycle or Tri Carboxylic Acid Cycle** (TCA). It takes place in **Mitochondria** where all the necessary enzymes for it are found on **cristae.** Various reactions of the Kreb's Cycle which is shown in Fig. 123. are as follow :

(11) Pyruvic acid reacts with CoA and NAD and is **oxidatively decarboxylated**. One mole. of CO_2 is released and NAD is **reduced.** Pyruvic acid is converted into **Acetyl CoA**.

$$\underset{\text{Pyruvic acid}}{CH_3CO{\cdot}COOH} + CoA + NAD \rightarrow \underset{\text{Acetyl CoA}}{CH_3CO{\cdot}CoA} + CO_2 + NADH_2$$

(In fact, the formation of Acetyl-CoA and $NADH_2$ involves a complex of enzymes and 5 cofactors *viz.*, coenzyme-A, thiamine pyrophosphate (TPP), NAD, Mg^{++}, and lipoic acid. Various steps of this reaction are as follow :—

(*i*) Pyruvic acid forms a complex with TPP and is decarboxylated.

(*ii*) Acetaldehyde part of the TPP-complex reacts with lipoic acid (oxidised) to form Acetyl-lipoic acid complex in which lipoic acid is present in reduced form. The TPP becomes free.

(*iii*) Acetyl-lipoic acid complex reacts with coezyme-A to form acetyl-CoA. Reduced lipoic acid is liberated.

(*iv*) Reduced lipoic acid reacts with oxidised NAD to form reduced $NADH_2$. Lipoic acid is oxidised again).

(12) Acetyl-CoA condenses with oxaloacetic acid in the presence of *condensing enzyme* and water molecule to form **citric acid.** CoA becomes free.

$$\begin{array}{l} CH_3CO\cdot CoA \\ \text{Acetyl-CoA} \\ \quad + \\ CO\cdot COOH \\ | \\ CH_2COOH \\ \text{Oxaloacetic acid} \end{array} \xrightarrow[+H_2O]{\textit{Condensing enzyme}} \begin{array}{l} CH_2COOH \\ | \\ C\ (OH)\ COOH + CoA \\ | \\ CH_2COOH \\ \text{Citric acid} \end{array}$$

(13) Citric acid is dehydrated in the presence of *Aconitase* to form **Cis-Aconitic Acid.**

$$\begin{array}{l} CH_2COOH \\ | \\ C(OH)COOH \\ | \\ CH_2COOH \\ \text{Citric acid} \end{array} \xrightarrow[-H_2O]{\textit{Aconitase}} \begin{array}{l} CH_2COOH \\ | \\ C\cdot COOH \\ \| \\ CHCOOH \\ \text{Cis-Aconitic acid} \end{array}$$

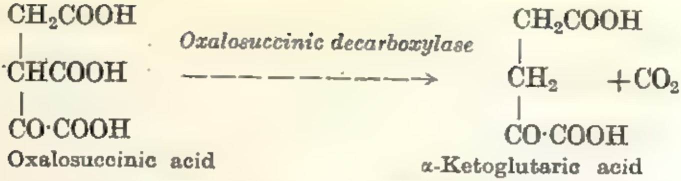
(14) Cis-Aconitic Acid reacts with one mole. of water to form **Ios-citric Acid.**

$$\begin{array}{l} CH_2COOH \\ | \\ C\cdot COOH + H_2O \\ \| \\ CH.COOH \\ \text{Cis-Aconitic Acid} \end{array} \rightarrow \begin{array}{l} CH_2COOH \\ | \\ CH.COOH \\ | \\ CHOH\cdot COOH \\ \text{Iso-Citric Acid} \end{array}$$

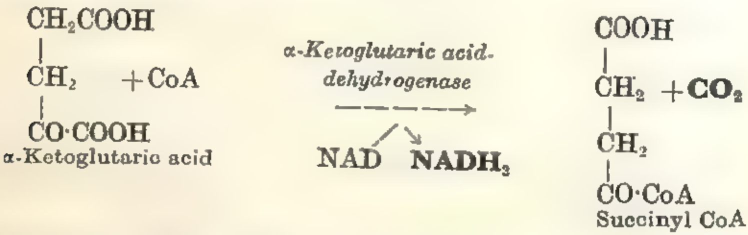
(15) Iso-Citric Acid is oxidised to **Oxalosuccinic acid** in the presence of *Isocitric-dehydrogenase.* Conzyme-II *i.e.,* **NADP is reduced** in the reaction.

$$\begin{array}{l} CH_2COOH \\ | \\ CH.COOH \\ | \\ CHOH.COOH \\ \text{Iso-Citric Acid} \end{array} \xrightarrow[NADP \ \nearrow\searrow \ NADPH_2]{\textit{Isoctiric-dehydrogenase}} \begin{array}{l} CH_2COOH \\ | \\ CH.COOH \\ | \\ CO\cdot COOH \\ \text{Oxalosuccinic acid} \end{array}$$

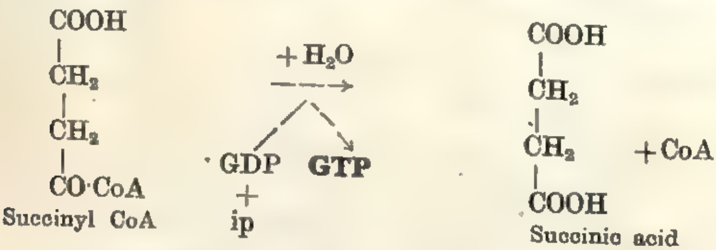
(16) Oxalosuccinic acid is **decarboxylated** in the presence of *Oxalosuccinic decarboxylase* to form α-**ketoglutaric acid**. A second mol. of CO_2 is released.



(17) α-Ketoglutaric acid reacts with CoA and NAD in the presence of *α-ketoglutaric acid-dehydrogenase* and is **oxidatively decarboxylated** to form **Succinyl CoA** and a third mol. of $\mathbf{CO_2}$ is released. **NAD is reduced** in the reaction.



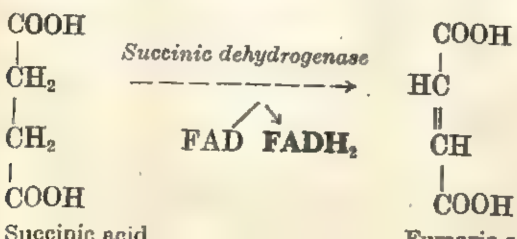
(18) Succinyl CoA reacts with water mol. to form **Succinic acid**. CoA becomes free and one mol. of GDP (Guanosine diphosphate) is phosphorylated in presence of inorganic phosphate to form one mol. of **GTP**.



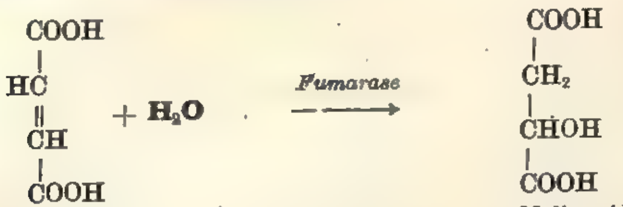
GTP may react with ADP to form one molecule of **ATP**.

GTP + ADP → **ATP** + GDP

(19) Succinic acid is oxidised to **Fumaric acid** in the presence of *Succinic dehydrogenase*. Coenzyme **FAD** (Flavin Adenine Dinucleotide) is **reducaed** in the reaction.



(20) One mol. of H_2O is added to Fumaric acid in the presence of *Fumarase* to form **Malic acid.**



Fumaric acid Malic acid

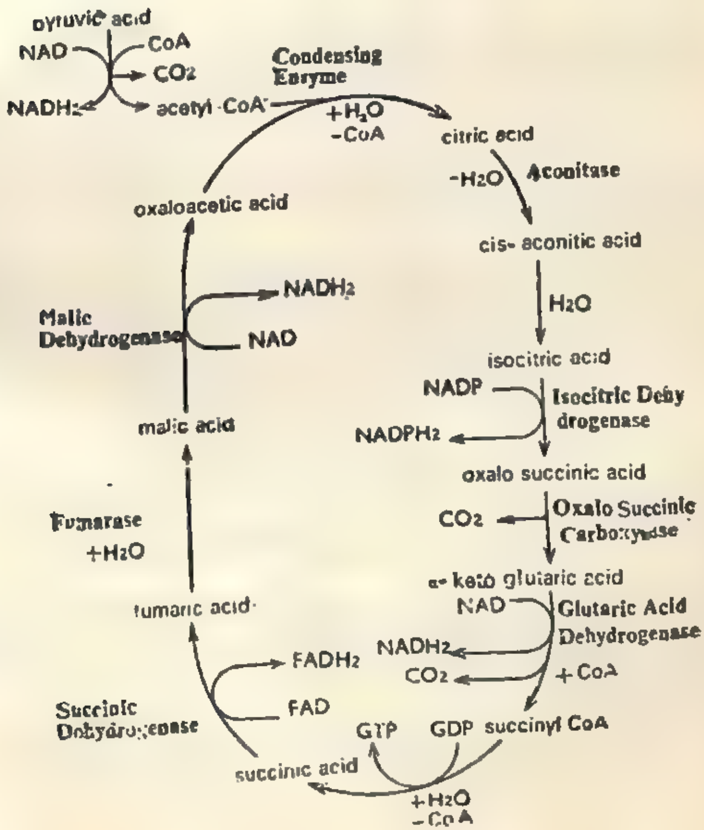


Fig. 72. Kreb's cycle

(21) In the last step Malic acid is oxidised to oxaloacetic acid in the presence of *Malic-dehydrogenase.* One mol. of coenzyme I, *i.e.*, **NAD** is reduced.

$$\begin{array}{l} COOH \\ | \\ CH_2 \\ | \\ CHOH \\ | \\ COOH \\ \text{Malic acid} \end{array} \quad \xrightarrow[\text{NAD} \quad \textbf{NADH}_2]{\textit{Malic dehydrogenase}} \quad \begin{array}{l} CO \cdot CCOH \\ | \\ | \\ CH_2COOH \\ \text{Oxaloacetic acid} \end{array}$$

In this cycle, at first the carbon atom 3 or 4, then 2 or 5, and lastly carbon number 1 or 6 of the glucose molecule are released in the form of CO_2 molecules.

(D) TERMINAL OXIDATION OF THE REDUCED COENZYMES OR ELECTRON TRANSPORT SYSTEM AND OXIDATIVE PHOSPHORYLATION

The last step in aerobic respiration is the oxidation of **reduced conezymes** produced in glycosis and Kreb's cycle by molecular oxygen through **FAD**, *cytochrome b*, *cytochrome c*, *cytochrome a* and *cytochrome* a_3 (*cytochrome oxidase*).

Two H-atoms or electrons from the reduced coenzyme ($NADH_2$ or $NADPH_2$) travel through FAD and the *cytochromes* each with a more positive oxidation—reduction potential* and ultimately combine with 1/2 O_2 molecule to produce one molecule of H_2O (Fig. 73). This is called as **terminal oxidation**.

During this **electron transport**, FAD and the **iron atom** of different cytochromes get successively reduced (Fe^{++}) and oxidised (Fe^{+++}) and enough energy is released at some places which is utilised in the **phosphorylation** of ADP molecules (in the presence of inorganic phosphate) to generate energy rich **ATP** molecules.

Because this oxidation accompanies phosphorylation, hence it is called as **oxidative phosphorylation**. It takes place on **stalked particles** situated on cristae in Mitochondria. It is inhibited by **2, 4-Dinitrophenol**.

One molecule of **ATP** (which contains 7·6 K. Cal. energy) is synthesized at each place when electrons are transferred from :—

(*i*) reduced $NADH_2$ or $NADPH_2$ to FAD,

(*ii*) reduced Cytochrome b, to Cytochrome c, and

(*iii*) reduced Cytochrome a to Cytochrome a_3.

---

* See foot-note on page 130. Redox potential (E'_0) values of some redox-systems are given below : NAD/NADH (−0·32 V), Cyt. b (−0·04 V), Cyt. c (+0·25 V), Cyt. a (+0·29 V), O_2 (+0·82 Volts).

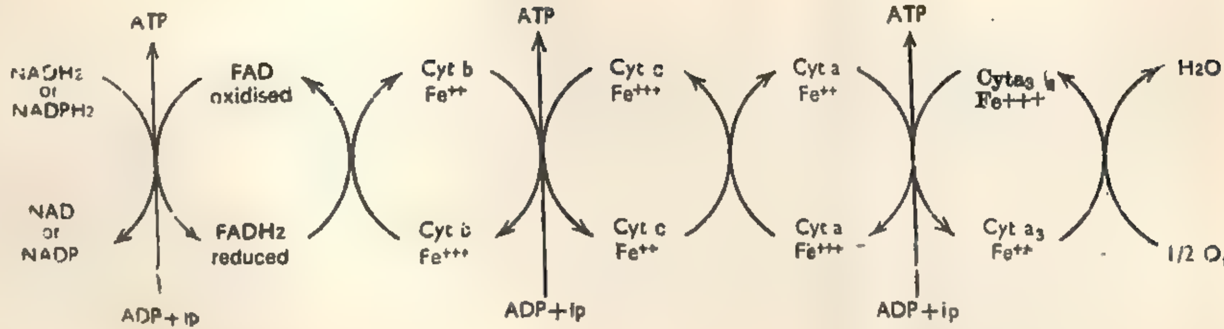


Fig. 73. Electron transport system and oxidative phosphorylation.

Thus, the oxidation of one mole. of reduced $NADH_2$ or $NADPH_2$ will result in the formation of **3 ATP** molecules while oxidation of $FADH_2$ will lead to the synthesis of **2 ATP** molecules.

Complete oxidation of a glucose mol cule (hexose sugar) results in the net gain of **38 ATP** molecules as shown in Table 9.

One glucose molecule contained about 686 K. Cal. energy. 38 ATP molecules will have 288·8 K. cal. energy. Therefore, about 40% (288·8/686) energy of the glucose molecule is utilised during aerobic breakdown, the rest is lost as heat.

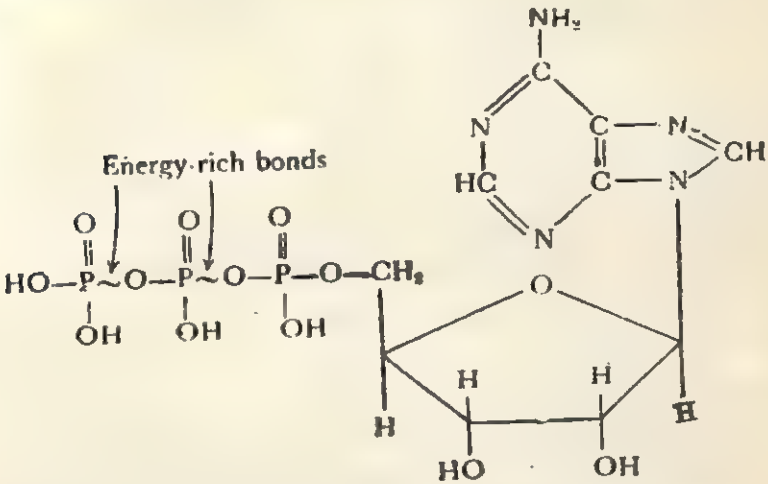
Because huge amount of energy is generated in **Mitochondria** in the form of **ATP molecules**, they are called as **Power Houses** of the cell.

Table 9. Account of ATP Molecules in Glycolysis and Kreb's Cycle

Reaction No.	Gain of ATP per hexose mol.	Consumption of ATP per hexose mol.	Net Result
Glycolysis			
1.	×	1	
3.	×	1	
6.	2×3=6	×	
7.	2×1=2	×	
10.	2×1=2	×	
	Total=10	Total = 2	Net Gain of 10−2=8 ATP mols.
Kreb's Cycle			
11.	2×3=6	×	
15.	2 · 3=6	×	
17.	2×3=6	×	
18.	2×1=2	×	
19.	2×2=4	×	
21.	2×3=6	×	
	Total=30	Total=0	Gain of 30 ATP mols.

Total net gain of ATP mol./hexose mol. oxidised.
8+30=38 ATP mols.

ATP molecules contain energy in terminal *pyro-phosphate* bonds When these energy rich bonds break, energy is released which is utilised in driving various other metabolical processes of the cell.



ATP (Adenosine triphosphate)

MODERN VIEW OF THE ELECTRON TRANSPORT SYSTEM AND OXIDATIVE PHOSPHORYLATION IN MITOCHONDRIA

According to the recent view the electron transport system in mitochondria consists of **4 complexes** which are found **in the bases of the stalked particles** and also **coenzyme-Q** (Ubiquinone) and

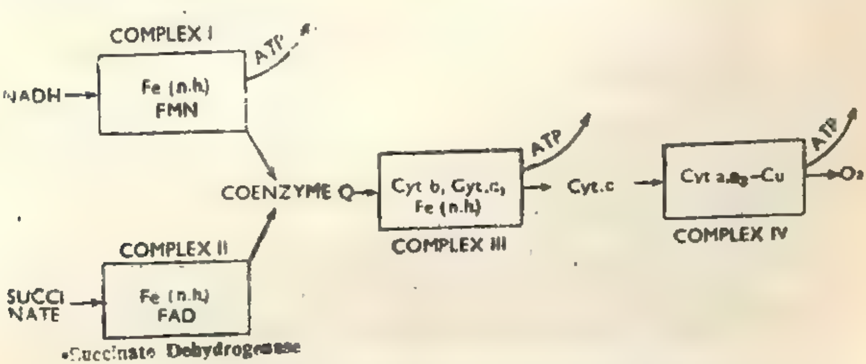


Fig. 74. Diagrammatic representation of the four complexes of the electron transport system and their functional arrangement.

cytochrome-C which are not bound to stalked particles but act as electron carriers between the complexes (Fig. 74).

Complex I consists of **FMN** (Flavin Mono Nucleotide) and non-heme iron (Fe—(n.h) and is responsible for passing electrons from $NADH_2$ or $NADPH_2$ to *coenzyme Q*. **Complex II** consists of *succinate dehydrogenase* which itself is a flavoprotein in which the prosthetic group is **FAD** (Flavin Adenine Dinucleotide) and contains non-heme iron. This complex receives electrons from succinic acid (which is oxidised in Kreb's cycle to form fumaric acid. See reaction no. 19) and passes them to *coenzyme-Q*. **Complex III** consists of *cytochrome b* containing non-heme iron and *cytochrome* c_1. This complex takes electrons from coenzyme-Q and passes them to *cytochrome c*. **Complex IV** consists of *cytochrome a* and *cytochrome* a_3 *i.e.*, *cytochrome oxidase* which contains **Cu**. This complex receives electrons from *cytochrome c* and transfers them to molecular oxygen so that H_2O molecules are produced (**terminal oxidation**).

Recent freeze cleavage studies have indicated that during the transfer of electrons from (*i*) Complex I to coenzyme-Q (*ii*) Complex III to *cytochrome C* and (*iii*) Complex IV to molecular oxygen, the head piece (F_1-ATPase) of the stalked particle is **tuked into the base** where it is able to work in close apposition to the complexes of the electron transport system (Fig. 75 B). During this **contracted or energised state oxidative phosphorylation** takes place. The energy released during the transfer of electrons is utilised in the formation of one ATP molecule from ADP in the presence of the enzyme *ATPase* (or F_1) which is associated with the head of the stalked particle. After the ATP molecule has been formed, the head of the stalked particle again comes in its normal state which is also called as **resting state** or **orthodox state** (Fig. 75 A).

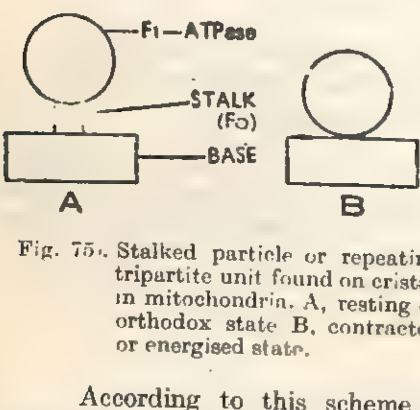


Fig. 75. Stalked particle or repeating tripartite unit found on cristae in mitochondria. A, resting or orthodox state B, contracted or energised state.

According to this scheme also, the terminal oxidation of the reduced coenzyme $NADH_2$ or $NADPH_2$ results in the formation of 3 ATP molecules while oxidation of $FADH_2$ will result in the synthesis of 2ATP molecules (Fig. 74).

(E) COUPLING OF PHOSPHORYLATION (ATP SYNTHESIS) TO ELECTRON TRANSPORT OR MECHANISM OF OXIDATIVE PHOSPHORYLATION

The mechanism involved in converting electron-flow energy into ATP is not yet clear. Three theories have been put forward to try to explain the mechanism of oxidative phosphorylation or coupling of phosphorylation (*i.e.*, ATP synthesis) to electron transport which are as follow :

1. The chemical coupling theory

This theory was first proposed by **Slater** in 1953 and is based on the principles of substrate-level phosphorylation as illustrated by reaction sequence for glyceraldehyde-3-phosphate dehydrogenase in glycolysis resulting in the formation of one ATP molecule and 3-phosphoglyceric acid. (For details see glycolysis).

According to this theory (Fig. 76) a reduced electron carrier of the respiratory chain (*e.g.*, $\mathbf{AH_2}$) reacts with an oxidised carrier (*e.g.*, **B**) which is adjacent to it with sufficient free energy drop occurring to allow the reaction of **A** with an unknown compound **C** to give a **non-phosphorylated high energy intermediate** Compound **A∼C**. **B** is reduced to $\mathbf{BH_2}$.

In the next sequential exchange reactions, **C** is transferred to phosphate to form a **phosphorylated intermediate C∼P**. The electron carrier **A** becomes free and oxidised.

Finally, phosphate from **C∼P** is transferred to ADP to give **ATP**. The unknown compound **C** becomes free and recycled.

Alternatively, there may be a parallel scheme of reactions in which the high-energy non-phosphorylated intermediate is formed with $\mathbf{BH_2}$ instead of **A** (Fig. 127).

(*i*) $AH_2 + B + C \rightleftharpoons A{\sim}C + BH_2$,

(*ii*) $A{\sim}C + Pi \rightleftharpoons C{\sim}\mathbf{P} + A$

(*iii*) $C{\sim}\mathbf{P} + ADP \rightleftharpoons ATP + C$

A and B are electron carriers. An alternative scheme can be proposed in which a high-energy intermediate $BH_2{\sim}C$ is formed instead of $A{\sim}C$.

(*i*) $AH_2 + B + C \rightleftharpoons A + BH_2{\sim}C$

(*ii*) $BH_2{\sim}C + Pi \rightleftharpoons C{\sim}\mathbf{P} + BH_2$

(*iii*) $C{\sim}\mathbf{P} + ADP \rightleftharpoons ATP + C$

Fig. 76. The chemical coupling theory.

The chemical coupling theory did not find much support because no phosphorylated intermediates or high-energy intermediates of the respiratory carriers have yet been identified unequivocally.

2. The conformational coupling theory

This theory was first put forward by **Boyer** in 1964 and according to this the free energy liberated during electron transport is conserved as a conformational change in the protein component of a respiratory electron carrier or complex of carriers and this change is associated in someway with the phosphorylation of ADP to form ATP.

Boyer suggested that conformational change in an electron carrier probably brought a carboxyl and sulphydryl group very close to each other to form an **acyl-s-linkage** (Fig. 128 A) and that this was the 'high-energy intermediate' which could drive ATP synthesis.

Based on conformational coupling theory **Green and ji (1972)** have given their **electromechanochemical** coupling theory which envisaged conformational changes in enzyme complexes rather than in individual carriers. According to their model the transport of electrons brings about a conformational change in one of the electron transport complexes in the form of **mechanical and electrical strain components**. Similar mechanical and electrical changes are in turn induced in an **ATPase Complex**. The reverse conformational change now leads to the synthesis of ATP bringing back the electron transport complex and the ATPase complex in their original form (Fig. 77 B).

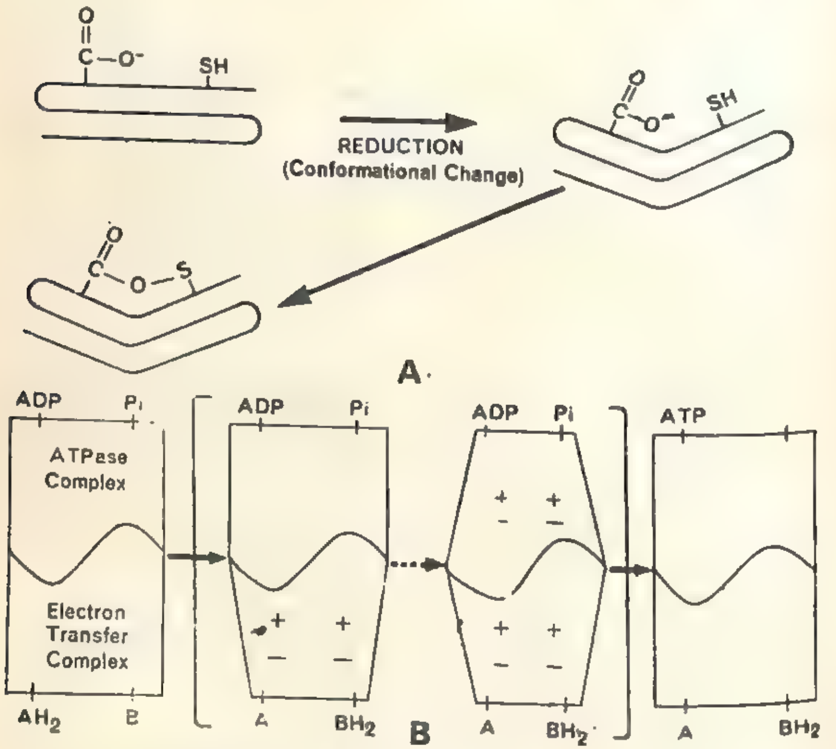


Fig. 77. Conformational coupling theory. A, Boyer's original theory. B, Green and Ji's electromechanochemical model.

Although, conformational coupling theory is quite attractive but main difficulty with this theory is the problem of setting up experiments to test it.

3. The chemi-osmotic coupling theory

This theory was first put forward by **Mitchell** in 1960 and is most convincing of all the three theories to explain the mechanism of

mitochondrial oxidative phosphorylation. It is also equally applicable to chloroplastic photophosphorylation.

The main feature of this theory (Fig. 78) is a **membrane-located reversible ATPase**. The membrane is mitochondrial in case of oxidative phosphorylation and chloroplastic in case of photo-phosphorylation.

The ATPase reversibly catalyses the following reaction :

$$ATP + H^+ + OH^- \rightleftharpoons ADP + Pi$$

This reaction is assumed to be **anisotropic** so that the active centre is accessible to **H**$^+$ but not OH$^-$ from the **outer side** of the membrane. On the other hand it is accessible only to **OH**$^-$ but not **H**$^+$ from the **inner side** of the membrane. The active centre is assumed to be relatively inaccessible to water and the membrane almost impermeable to ions.

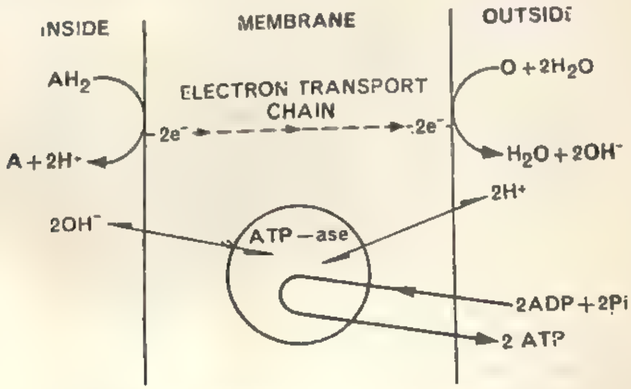


Fig. 78. Mitchell's chemi-osmotic hypothesis.

It is quite obvious from the ATPase catalysed reversible reaction that the removal of H$^+$ and OH$^-$ would favour the reaction towords ATP synthesis. According to **Mitchell** H$^+$ and OH$^-$ can be removed by membrane bound electron transport chain and the operation of ATPase in the following way :—

● The oxidation of the reduced electron carrier *e g.*, **AH**$_2$ to **A** with the simultaneous reduction of **O** to **H**$_2$**O** leads to the **accumulation** of H$^+$ on the inner side and OH$^-$ on the outer side of the membrane.

● These accumulations of H$^+$ on the inner side of the membrane **pull** OH from the ATP-ase catalysed reaction. Similarly, accumulations of OH$^-$ on the outer side of the membrane pull H$^+$ from the ATP-ase catalysed reaction. Thus, the equilibrium is shifted in favour of ATP synthesis (Fig. 78). The dehydrating force which

drives the ATP-ase catalysed reaction in the direction of ATP synthesis is derived from the chemical potential differential of the OH and H^+ across the membrane.

Mitchell's hypothesis also predicted the existence of **membrane transporters** or **specific exchange diffusion carriers** which has been shown to be correct. These carriers permit reversible exchange of anions (*e.g.* Cl^-) for OH^- and cations (*e.g.*, K^+) for H^+ and regulate the pH and osmotic differential across the membrane. These systems permit the movements of essential metabolites without breaking the membrane potential which is essential for ATPase catalysed reaction in the direction of ATP synthesis.

SIGNIFICANCE OF KREB'S CYCLE

Kreb's cycle occupies a central and very important place in the metabolism of plants.

(*i*) It provides energy in the form of ATP molecules (through oxidative phosphorylation) for various metabolical activities.

(*ii*) It is directly related with **Nitrogen Metabolism**. (α-ketoglutaric acid, an intermediate of Kreb's Cycle is the first acceptor molecule of NH_3 forming an amino acid, the glutamic acid. It is from the glutamic acid that various **transamination** reactions begin to form different **amino acids** which ultimately condense to form **proteins**.

(*iii*) It is also intimately related with **Fat Metabolism**. (Dihydroxyacetone phosphate produced in glycolysis may be converted into glycerol via α-glycerophosphate and *vice versa*. Glycerol is important constituent of fats.

After β-oxidation, fatty acids give rise to active 2-C units, the **Acetyl CoA** which may enter the Kreb's Cycle.)

(*iv*) It is closely associated with **Glyoxylate cycle**

(*v*) Other metabolic processes are related to Kreb's Cycle through its intermediates in one or the other way.

Although glycolysis is the principal route of the conversion of carbohydrates into pyruvic acid in many biological systems, it is by no means the only known metabolic route for breakdown of carbohydrates.

It has been observed that inhibitors such as **Iodoacetate, Fluorides, arsenates** etc., which specifically inhibit some steps of glycolysis, do not inhibit glucose utilization completely. This has led to the discovery of some other **alternative routes of carbohydrate breakdown** existing in plants, some animal tissues and several

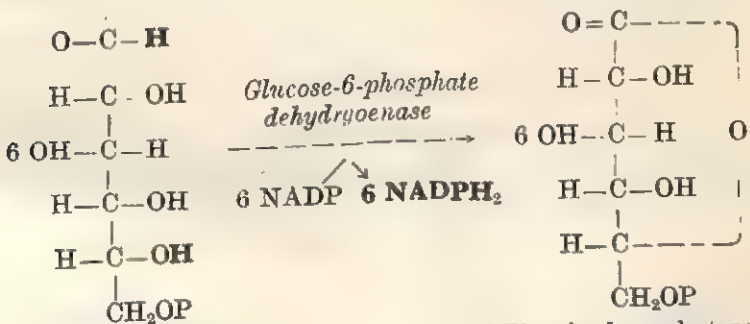
types of micro-organisms. One such very common alternative route in plants is **Pentose Phosphate Pathway**.

PENTOSE PHOSPHATE PATHWAY (WARBURG-DICKENS PATHWAY)

It involves the oxidation of Glucose-6-Phosphate to 6-Phosphogluconic acid which in turn is converted into **pentose phosphates**. In this pathway glucose-6-phosphate is directly oxidised without entering glycolysis, hence it is also known as **Direct Oxidation Pathway** or **Hexose Monophosphate Shunt**.

Starting from 6-molecules of glucose-6-phosphate, the various reactions of this pathway (Fig. 79) can be summarised as follow :

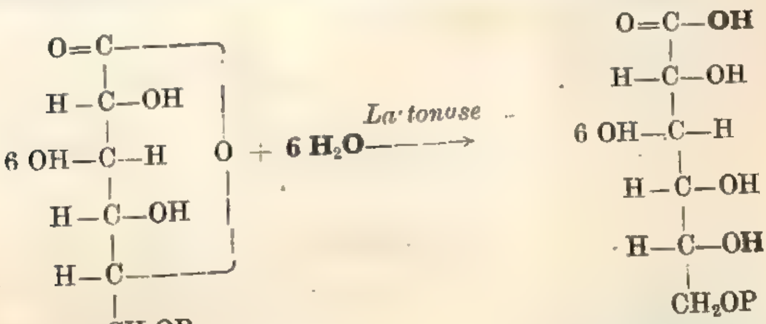
(1) 6 molecules of glucose-6-phosphate in the presence of coenzyme NADP are converted (oxidised) into 6 molecules of **6-phosphogluconolactone** by the enzyme *glucose-6-phosphate dehydrogenase*. 6 molecules of **NADP** are **reduced** in the reaction.



Glucose-6-phosphate

6-Phosphogluconolactone

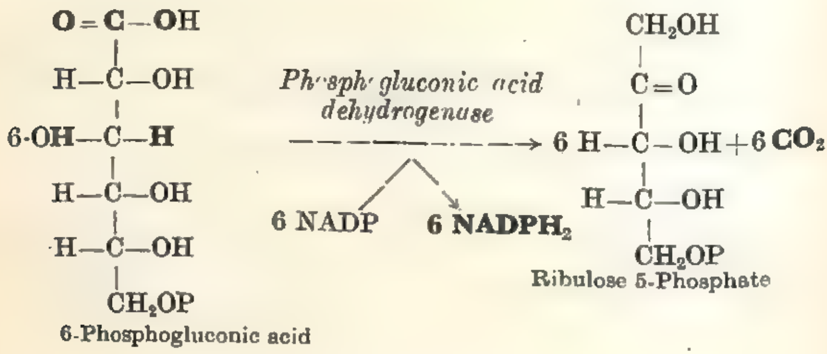
(2) 6-Phosphogluconolactone is hydrolysed by the enzyme *Lactonase* to produce 6 molecules of **6-phosphogluconic acid**.



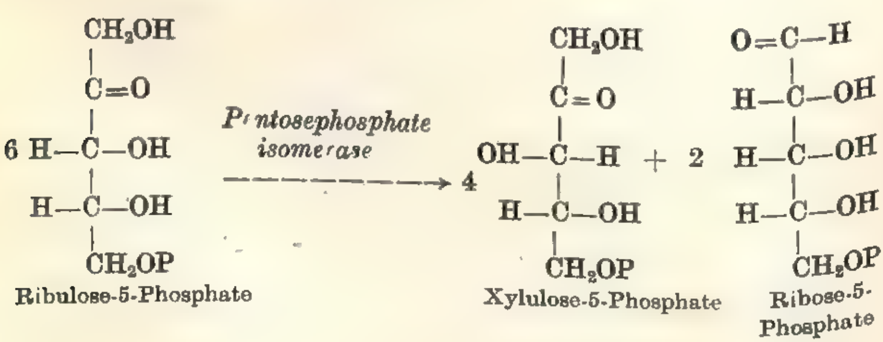
6-Phosphoguconolactone

6-Phosphogluconic acid

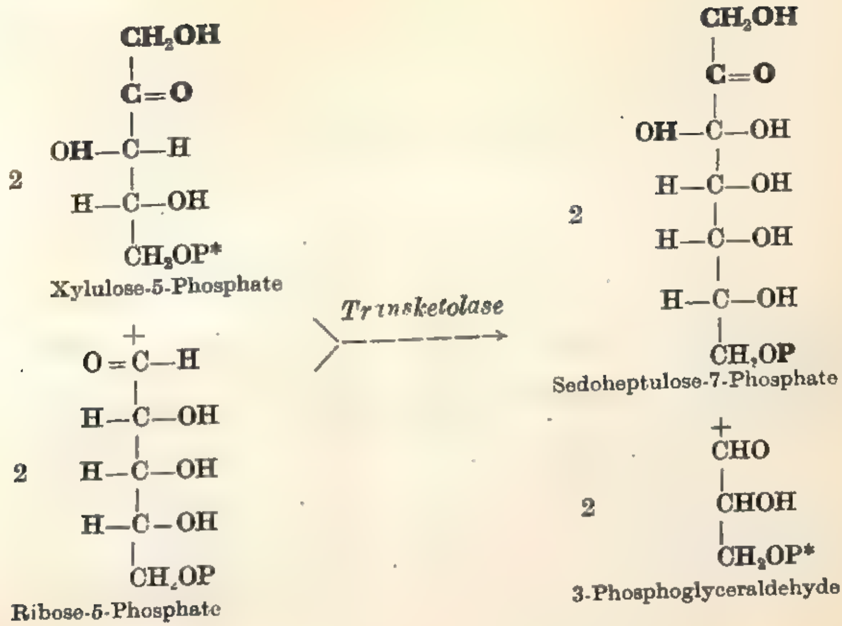
(3) 6-Phosphogluconic acid is **oxidatively decarboxylated** by the enzyme 6-*Phosphogluconic acid dehydrogenase*. 6 molecules of **NADP are reduced**, 6 molecules of CO_2 are released and 6 mols. of **Ribulose-5-Phosphate** are produced.



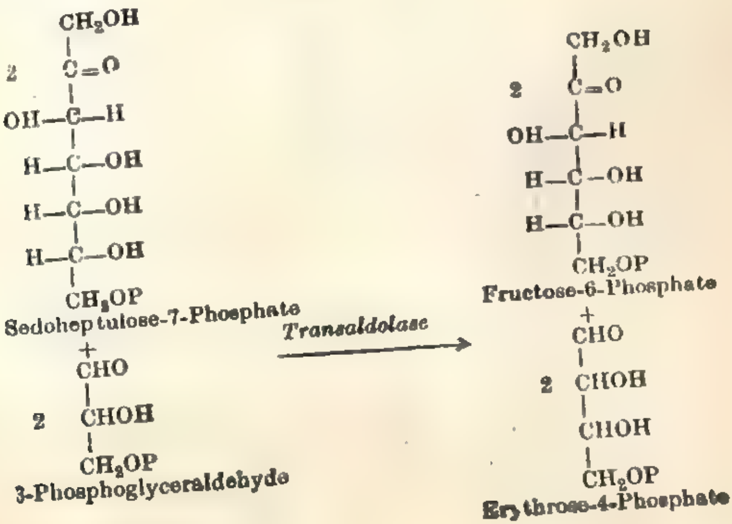
(4) 6 mols. of Ribulose-5-P isomerise into 4 mols of **Xylulose-5-Phosphate** and 2 mols. of **Ribose-5-Phosphate** in the presence of *Pentose phosphate isomerase*



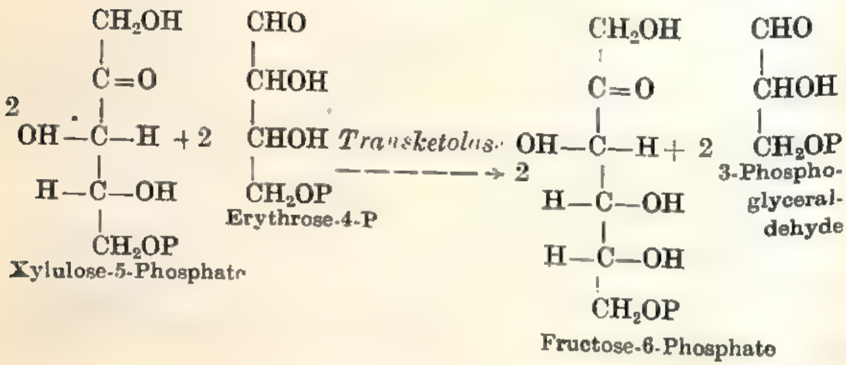
(5) 2 mols. of xylulose-5-Phosphate and 2 mols. of Ribose 5-phosphate combine in the presence of *Transketolase* to form 2 mols. of **Sedoheptulose-7-Phosphate** and 2 mols. of **3-Phosphoglyceraldehyde.**



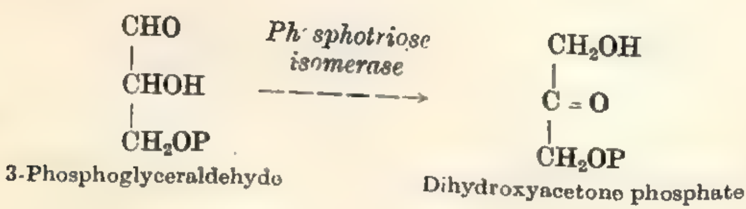
(6) 2 mols. of Sedoheptulose-7-Phosphate and 2 mols. of 3-Phosphoglyceraldehyde combine in the presence of *Transaldolase* to form **2 mols. of Fructose-6-Phosphate** and 2 mols. of **Erythrose-4-Phosphate** (4-carbon atoms sugar).



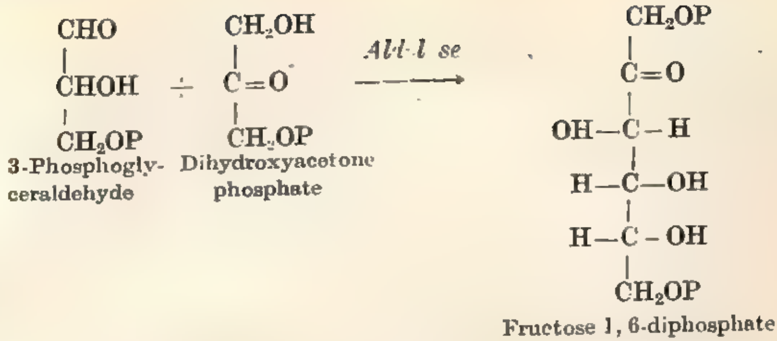
(7) 2 mols. of Erythrose-4-Phosphate react with remaining two mols. of xylulose-5-Phosphate (see reaction No. 4 and 5) in the presence of *Transketolase* to form 2 mols. of **Fructose-6 Phosphate** and 2 mols. of **3-Phosphoglyceraldehyde**.

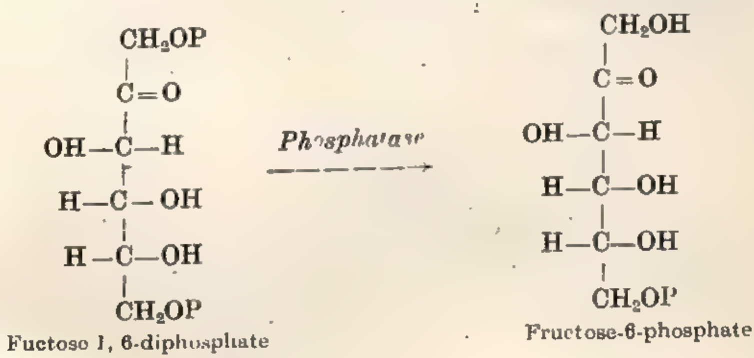


(8) One mol. of 3-phosphoglyceraldehyde isomerises into **dihydroxyacetone phosphate**. The enzyme is *Phosphotriose isomerase*.

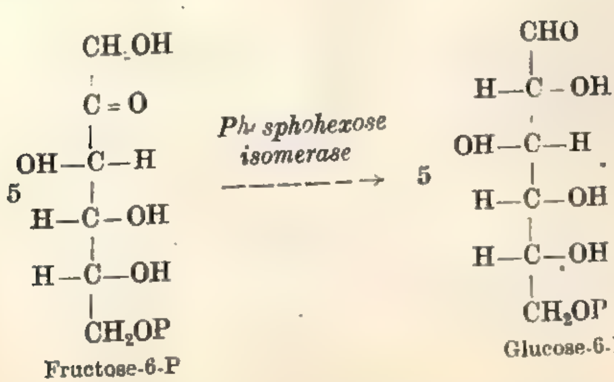


(9) Remaining one mol. of 3-Phosphoglyceraldehyde unites with Dihydroxyacetone phosphate in presence of *Aldolase* to form one mol. of **Fructose 1, 6-diphosphate**. The latter, in the presence of *Phosphatase* forms one mol. of **Fructose 6-Phosphate**.





(10) 5 molecules of Fructose-6-phosphate produced in reactions 6, 7 and 9, isomerise into 5 mols. of **Glucose-6-P** in presence of *Phosphohexose isomerase*.



To summarise, 6 mols. of Glucose-6-P which enter into this pathway, after oxidation produce **6 mols. of CO_2** (Reaction No. 3.

CO_2 comes from C-No. 1 of the glucose molecule) and **12 mols.** of reduced coenzymes **$NADPH_2$** reaction 1, 3) while **5 mols. of Glucose-6-Phosphate** are **regenerated** (Reaction No. 10).

$$6\ (\text{Glucose-6-P}) + 12\ NADPH_2 \rightarrow 5\ (\text{Glucose-6-P}) + 12\ NADPH_2 + 6\ CO_2$$

In other words, one mol. of Glucose-6-P after oxidation produced 6 mols. of CO_2 and 12 $NADPH_2$ molecules.

$$\text{Glucose-6-P} \xrightarrow{12\ NADP} 6\ CO_2 + 12\ NADPH_2$$

12 reduced coenzymes ($NADPH_2$) will yield **36 ATP** mols. by **oxidative phosphorylation** as in case of aerobic respiration.

SIGNIFICANCE OF PENTOSE-PHOSPHATE-PATHWAY

(*i*) It provides **alternative route** for carbohydrate breakdown and provision of **energy**.

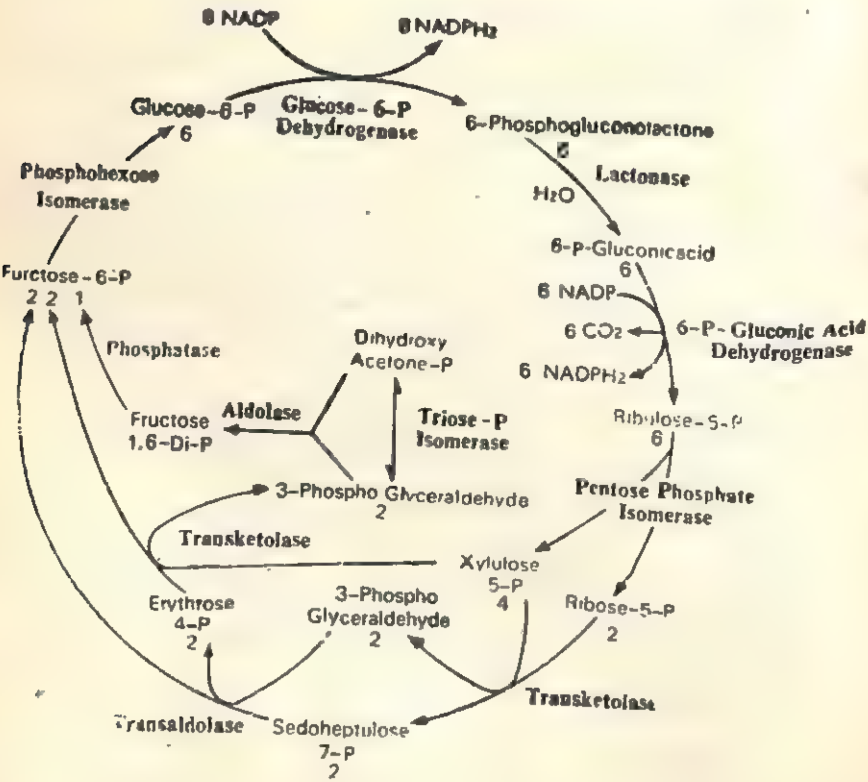


Fig. 79. Pentose phosphate pathway.

(ii) Provides **Ribose** sugars for the synthesis of **nucleic acids**.

(iii) Plays important role in **fixation of CO_2** in **photosynthesis** through **Ribulose-5-Phosphate**. (Ribulose 1, 5-Diphosphate derived from Ribulose-5-Phosphate is the primary acceptor of CO_2 in photosynthesis).

(In addition to the above pathway for the oxidation of carbohydrates, still other routes have been identified in some micro-organisms and enzyme systems discovered. In all such cases the initial steps of glucose oxidation differ from glycolysis but ultimately pyruvic acid is produced.

One such alternative pathway is **Entner Doudoroff Pathway** which is shown in Fig. 131. In this pathway the carboxylic group of pyruvic acid is derived from carbon No. 1 of glucose molecule (in glycolysis it was derived from C-No. 3 or 4)

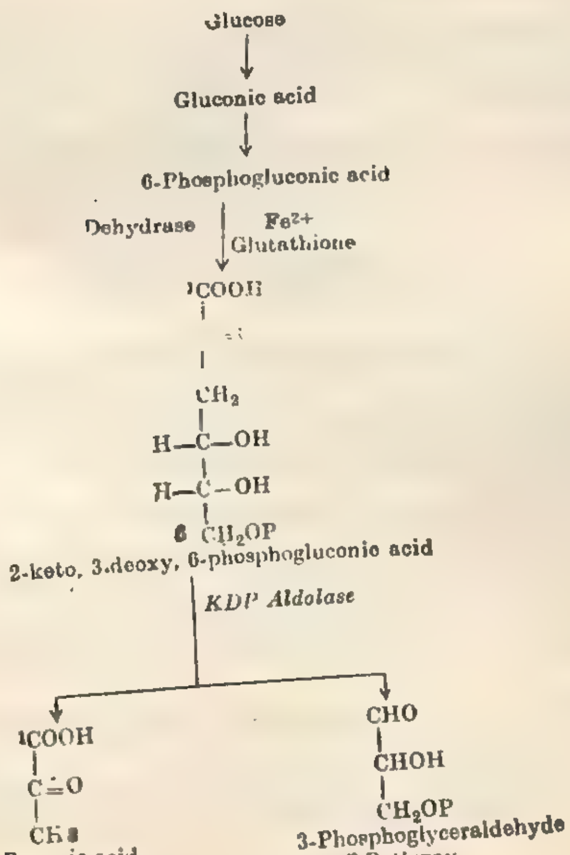


Fig. 80. Entner-Doudoroff Pathway.

RESPIRATORY QUOTIENT

The ratio of the volume of CO_2 released to the volume of O_2 taken in respiration is called as **respiratory quotient** and is denoted as **R.Q**.

$$R.Q. = \frac{\text{Vol. of } CO_2}{\text{Vol. of } O_2}$$

VALUE OF R.Q.

The value of R. Q. depends upon the nature of the **respiratory substrate** (the organic food matter oxidised in respiration) **and its oxidation.**

(1) When **carbohydrates** such as **hexose sugars** are oxidised in respiration, the value of R. Q. is 1 or **unity** because vol. of CO_2 evolved equals to the vol. of O_2 absorbed as is shown by the following equation

$$\underset{\text{Glucose}}{C_6H_{12}O_6} + 6O_2 \rightarrow 6CO_2 + 6H_2O$$

$$R.\ Q. = \frac{\text{vol. of } CO_2}{\text{vol. of } O_2} = \frac{6}{6} = 1 \text{ or unity.}$$

(2) When **fats** are the respiratory substrate, the value of R.Q. becomes **less than one** because the fats are **poorer in oxygen** in comparison to carbon and they require more O_2 for their oxidation which is obvious from the following equation :—

$$\underset{\text{Tripalmitin}}{2C_{51}H_{98}O_6} + 145O_2 \rightarrow 102\ CO_2 + 98\ H_2O$$

$$R.\ Q. = \frac{\text{vol. of } CO_2}{\text{vol. of } O_2} = \frac{102}{145} = 0.7 \text{ (less than one)}$$

(Fats are oxidised in respiration usually during the germination of fatty seeds).

(3) When **organic-acids** are oxidised in respiration the value

or R.Q becomes **more than one**. It is because organic acids are **rich in** O_2 and require less O_2 for their oxidation *e.g.*,

$$\underset{\text{Malic acid}}{C_4H_6O_5} + O_2 \rightarrow 4CO_2 + 3H_2O$$

$$R.Q. = \frac{\text{vol. of } CO_2}{\text{vol. of } O_2} = \frac{4}{3} = 1.3 \text{ (more than one)}$$

(4) Partial oxidation of carbohydrates

In some succulent plants* like *Opuntia*, carbohydrates are incompletely oxidised to organic acids **in dark** without the evolution of CO_2, hence the value of R.Q. remains O.

$$\underset{\text{Glucose}}{2C_6H_{12}O_6} + 3O_2 \rightarrow \underset{\text{Malic acid}}{3C_4H_6O_5} + 3H_2O$$

$$R.Q. = \frac{\text{vol. of } CO_2}{\text{vol. of } O_2} = \frac{0}{3} = 0.$$

(5) During **anaerobic respiration**, due to the absence of O_2 the value of R.Q. is always very high.

$$\underset{\text{Glucose}}{C_6H_{12}O_6} \rightarrow 2CO_2 + \underset{\text{Alcohol}}{2C_2H_5OH}$$

$$R.Q. = \frac{\text{vol. of } CO_2}{\text{vol. of } O_2} = \frac{2}{0}$$

SIGNIFICANCE OF R.Q.

By determining the value of R.Q. the nature of the **respiratory substrate** can be known. For example, if the value of R.Q is one, it indicates that carbohydrates are being oxidised during respiration. Similarly, if the value is less than one it will be concluded that organic matter like fats constitute the respiratory substrate.

* Actually in these plants which show **Crassulacean Acid Metabolism** the CO_2 produced at night during respiration is utilised in the synthesis of organic acids.

FACTORS AFFECTING RESPIRATION

A. INTERNAL FACTORS

(1) **Protoplasmic Factors.** The **amount of protoplasm** in the cells and its **state of activity** influence rate of respiration. (i) Rate of respiration is higher in young meristematic cells which divide actively and require more energy. Such cells have greater amount of protoplasm, there being no vacuoles. (ii) In older mature tissues, the rate of respiration is lower because of lesser amount of not very active protoplasm.

(2) **Concentration of the Respiratory Substrate.** Other factors being favourable, increased conc. of respirable food material brings about an increase in the rate of respiration.

B. EXTERNAL FACTORS

(1) **Temperature.** It has profound influence on the rate of respiration. **Optimum** temperature for respiration is about 30°C, **Minimum** 0°C, and **Maximum** about 45°C. At low temperatures the **respiratory enzymes** become inactive, consequently the rate of respiration falls. (It is due to this fact that the quality of fruits and vegetables stored at low temperature does not deteriorate).

An increase in temperature from 0° to 30°C or more brings about an **increased rate of respiration**, the $\mathbf{Q_{10}}$ for respiration being 2·5.

But at very high temperatures, respiration slows down and may even be stopped due to the **denaturation** of the respiratory enzymes.

(2) **Oxygen.*** In complete absence of oxygen **anaerobic respiration** takes place while aerobic respiration stops. (except in anaerobic organisms, the continued absence of O_2 for very long periods will ultimately cause death of the organism).

If some amount of O_2 is available, **aerobic respiration** will start and anaerobic respiration will slow down.

When sufficient amount of O_2 is available, the rate of aerobic respiration will be optimum while anaerobic respiration will be completely stopped. (This is called as **Extinction Point**).

* See also Pasteur's effect.

(3) **Carbon dioxide**. Higher conc. of CO_2 in the atmosphere especially in the poorly aerated soil, has retarding effect on the rate of the respiration.

(4) **Inorganic salts**. It has been observed that if a plant or tissue is transferred from water to salt solution, the rate of respiration increases (It is called as 'Salt Respiration').

(5) **Water**. Proper hydration of respiring cells is essential for respiration. Rate of respiration decreases with decreased amount of water, so much so, that in dry seeds the respiration is at its **minimum**. It is because in absence of a **medium** (provided by water) the respiratory enzymes become inactive.

(6) **Light**. Its effect is indirect on the rate of respiration through the synthesis of organic food matter in photosynthesis.

(7) **Injury**. Wounding of plant organs stimulates respiration in that organ. (Cells at the injured portion become meristematic to form new cells to heal up the wound, hence they require more energy which is supplied by increased rate of respiration). After the wound is healed up, the rate of respiration becomes normal.

LIGHT COMPENSATION POINT

It is well known that in green plants respiration occurs continuously for 24 hours while photosynthesis occurs only during the day when light is available. Some of the organic matter produced during photosynthesis is oxidised during respiration while rest is stored by the plant. It is implied from this that the photosynthesis is a faster process than respiration. We also know that the rate of photosynthesis is higher at about noon when light intensity is higher and is slower during morning or evening when light intensity is low. Obviously, there will be a time either in the morning or evening when the rate of photosynthesis will be as low as to equal the rate of respiration. This is called as **light compensation point**.

PASTEUR'S EFFECT

In his studies on alcoholic fermentation **Pasteur** in 1861 found that under anaerobic conditions much more sugar was taken up per quantity of yeast present than was consumed in the presence of O_2 (or aerobic conditions). This inhibition by O_2 of the rate of carbohydrate breakdown is often called as **Pasteur's effect**. Previously the existence of this effect was known only in yeasts and animal tissue but now this is also known to be operative in a variety of tissues of higher plants *e.g.*, barley leaves, apple fruits, potato tuber's carrot roots etc.

Although, the rate of the breakdown of carbohydrates (*i.e.*, respiratory substrates) is decreased by a shift to aerobic conditions, the energy made available in the form of ATP molecules is much

more. This is because of the greater efficiency of the aerobic rather than anaerobic respiration as an energy source in the cells. (One molecule of glucose for example yields 24 ATP molecules in aerobic respiration while only two ATP molecules are synthesised per glucose molecule oxidised anaerobically). In other words to perform a given amount of work, a tissue operating aerobically might be expected to oxidise much less glucose than in anaerobic work. It has in fact been observed that under anaerobic conditions the rate of consumption of carbohydrates by muscle tissue is app. 6—8 times to that observed under aerobic condition indicating thereby that the operation of aerobic mechanism of carbohydrate breakdown inhibits the rate of conversion of glucose to pyruvate.

The Pasteur's effect, therefore, appears to be an expression of the close interrelation between the cellular mechanisms of anaerobic glycolysis (responsible for the conversion of glucose to pyruvate) and of the citric acid cycle which causes the generation of ATP by aerobic breakdown of pyruvate through oxidative phosphorylation. This viewpoint has been supported by the findings that the Pasetur's effect is counteracted in yeast and other organisms by the "uncoupling" agent **2, 4—dinitrophenol** which is a well known inhibitor of mitochondrial oxidative phosphorylation.

One way in which the close interrelation of mitochondrial oxidative phosphorylation and glycolytic process may be mediated lies in their common dependence upon ADP as an acceptor of phosphate. Thus inhibition of mitochondrial phosphorylation of ADP would result in a higher concentration of this compound available to the ADP requiring glycolytic process. Similarly, there is competition between these two processes for inorganic phosphate, the latter having important direct effects upon glycolytic systems.

12

Growth and Growth Hormones

GROWTH

DEFINITION, REGIONS OF GROWTH AND GROWTH CORRELATIONS

Growth in a plant is the outcome of cell division, enlargement of the new cells and their differentiation into different types of tissues. These processes of growth are accompanied by (*i*) a permanent change in size (usually an increase in length or volume) and (*ii*) an increase in the dry weight of the growing parts.

In plants growth is confined only to **meristems**. The extreme apices of root and shoot, for instance are occupied by **primary meristems** while in their older parts, **secondary meristems** (*i.e.*, cambia) give rise to additional vascular tissues and to protective layers of cork cells.

The activity of each meristem influences the activity of the other meristems especially those near to it, giving rise to what is called as **growth correlations**. For instance, while the main apical shoot meristem is active it retards the activity of more recently initiated lateral bud meristems, a phenomenon usually referred to as 'apical dominance.'

THE COURSE OF GROWTH (GRAND PERIOD OF GROWTH) OR SIGMOID CURVE (GRAND PERIOD CURVE)

Usually under favourable conditions there is a characteristic course of increase in the plant in any of its growing parts. Growth is slow at first (Lag Phase), then gains speed (Log Phase), and eventually slows down (Descreasing Growth Rate) to come to a halt

(Steady State). The total time during which this course of growth takes place is called as the **Grand Period of Growth.** If this growth rate is plotted against time, a S shaped curve is obtained which is called as **Sigmoid Curve** or **Grand Period Curve** (Fig. 81).

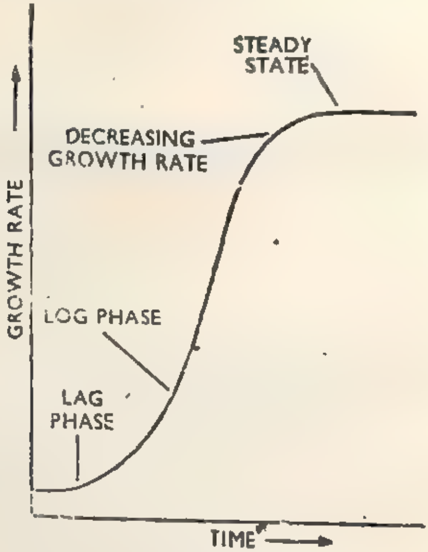


Fig. 81. Sigmoid curve.

The sigmoid curve represents the integrated sum of the curves for each growing organ and cell and presents the changing size of these parts. Similarly, when dry weight is measured as an index of growth before maturity, the curve takes the well known sigmoid form. Environmental conditions may alter growth rates but not the sigmoid form of the growth curve.

MEASUREMENT OF GROWTH

Growth in plant can be measured in terms of either (*i*) an increase in length or girth as in case of stem and root, or (*ii*) an increase in weight, or (*iii*) an increase in volume or area as in case of fruits and leaves respectively. The following methods are usually employed for the measurement of growth in length :—

(1) Direct Method :

This is the most simple rather crude method of the measurement of growth in which the length of the growing part is measured just by the help of a scale after intervals.

(2) Horizontal Microscope :

In this method, a point is marked near the stem or the root tip and is focussed by horizontal microscope which slides over a

graduated vertical stand (Fig. 82). After some time the same point is again focussed either by raising (in case of stem tip) or lowering (in case of root tip) the horizontal microscope. The difference of the initial and final readings on the graduated vertical stand measures the growth of stem or the root tip in length.

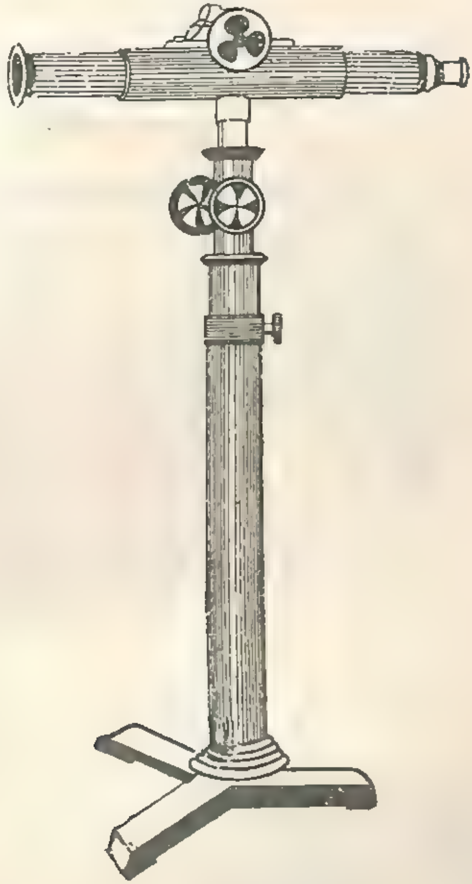


Fig. 82. Horizontal microscope.

(3) Arc Auxanometer :

The increase in length of the stem tip can easily be measured by an arc auxanometer which consists of a small pulley to the axil of which is attached a long pointer sliding over a graduated arc as shown in the Fig. 83. A thread, one end of which is tied to the stem tip and the other end to a weight passes over the pulley tightly. As soon as the stem tip increases in length, the pulley moves and the pointer slides over the graduated arc. The reading is taken. Actual increase in length of the stem is then calculated by knowing the length

of the pointer and the diameter of the pulley. If the diameter of the pulley is 4" and the length of the pointer 20", growth is magnified ten times on the graduated arc.

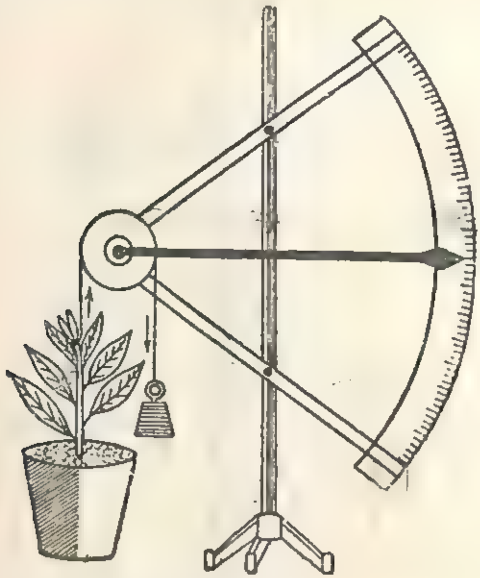


Fig. 83. Arc Auxanometer.

(4) **Pffefer's Auxanometer** :

It consists of a compound pulley with a small and a large wheel both having the same axil. A thread, one end of which is tied to the

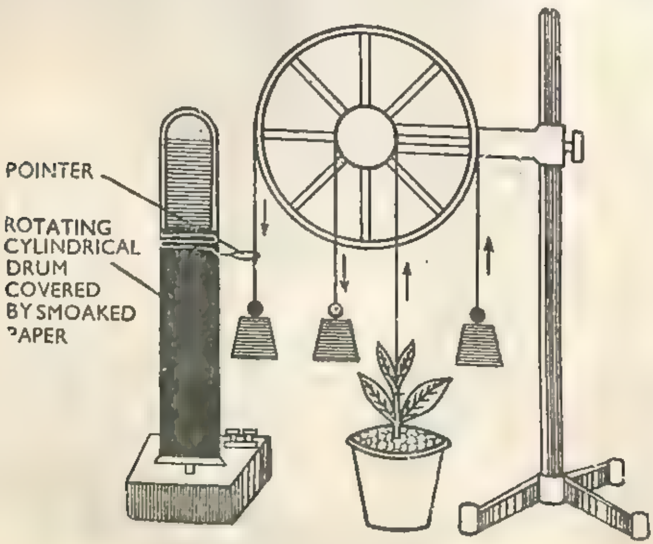


Fig. 84. Pffefer's auxanometer.

stem tip and the other end to a weight passes over the smaller wheel tightly. Another thread whose both ends are tied with weights tightly passes over the larger wheel. Near one end of this thread is attached a pointer which remains in touch with a rotating cylindrical drum covered by a smoaked paper as shown in the Fig. 84. As soon as the stem tip increases in length, the wheels of the pulley move so that the pointer also moves downward and traces a special white marking on the smoaked paper which gives an idea of the growth in the stem tip. Actual increase in length of the stem can be calculated by knowing the radii of larger and smaller wheels and the rate of rotation of the drum.

NATURAL GROWTH HORMONES IN PLANTS

Most of the physiological activities and growth in plants are regulated by the **action and interaction** of some chemical substances in them called as **hormones** and by certain naturally occurring **inhibitors** *e.g.*, phenols, flavonols and abscisic acid. To distinguish them from the animal hormones they are termed as **phytohormones**. According to **Pincus and Thimann** (1948) a plant hormone is defined as **"organic substance produced naturally in the higher plants, controlling growth or other physiological functions at a site remote from its place of production and active in minute amounts."**

These phytohormones have also been termed as growth hormones, growth promoting substances, growth substances, growth factors, growth regulators etc., by various workers and defined accordingly.

The **auxins** were the first hormones to be discovered in plants and at one time considered to be the only naturally occurring plant growth hormones. Since then besides other less important hormones, two important groups of chemical substances having profound influence on the regulation of growth and development in plants, have been discovered which are also considered as **natural plant growth hormones**. They are **Gibberellins** and **Cytokinins**.

Although the role of the above growth hormones is now well established in vascular plants, their role in the non-vascular plants is less clear.

1. THE AUXINS

DISCOVERY AND CHEMICAL NATURE

The discovery of auxins dates back to last quarter of the 19th century when **Charles Darwin** was studying tropisms in plants. He exposed grass coleoptile to unilateral light and observed it to bend towards light. He covered the coleoptile tip with tin foil or cut it off

so that it was not acted upon by light and observed that the coleoptile did not bend towards unilateral light. Thus he concluded from his experiments that some **'stimulus'** is transmitted from upper to the lower part which induced bending of the coleotile. These observations are recorded in his famous-book on the **"Power of Movement in Plants"** (1880).

(**Coleoptile.** In Monocots e.g., grasses, oats, maize etc,, the plumule in the seed remains covered by a protective cap like structure called as **coleoptile.** On germination of the seed, the coleoptile grows upward in the form of a tubular covering which surrounds the long narrow primary leaf during early stages of the development of the seedling as shown in figure 144. After some time, the coleoptile does not keep pace with the rapidly growing primary leaf which comes out of the coleoptile after piercing its tip and becomes exposed).

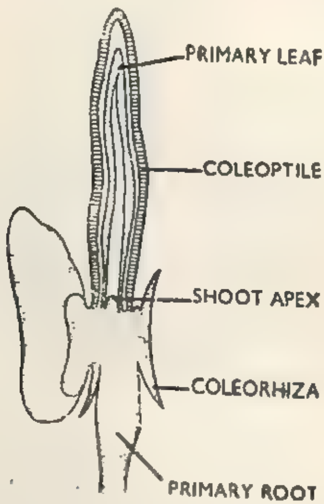


Fig. 85. L. S. of the Oat (*Avena sativa*) seedling.

Many years later, **Boysen-Jensen** (1910) cut off the coleoptile tip and replaced it with a thin plate of gelatine inserted between the tip and cut stump and observed that the coleoptile could still bend towards unilateral light. Although he did not give any explanation, but it was evident from his experiment that the **'stimulus'** mentioned by **Darwin** was in fact a **'material substance'** which was in control of growth.

The explanation was given by **Paal** (1919) who cut off the tip of the coleoptile and replaced it asymmetrically on the cut coleoptile stump and discovered that the coleoptile bent away from the side bearing tip even in dark. Thus he concluded that the tip secretes a substance which promotes the growth of the part below it. When

the tip is intact and receiving uniform light from all sides the growth is symmetrical. Therefore, the asymmetrical growth of the coleoptile resulting in curvature towards unilateral light must have been due to an asymmetrical distribution of this growth substance (now known as auxin). Larger amounts of this substance on the shaded side cause that side to grow more and the coleoptile to bend towards unilateral light.

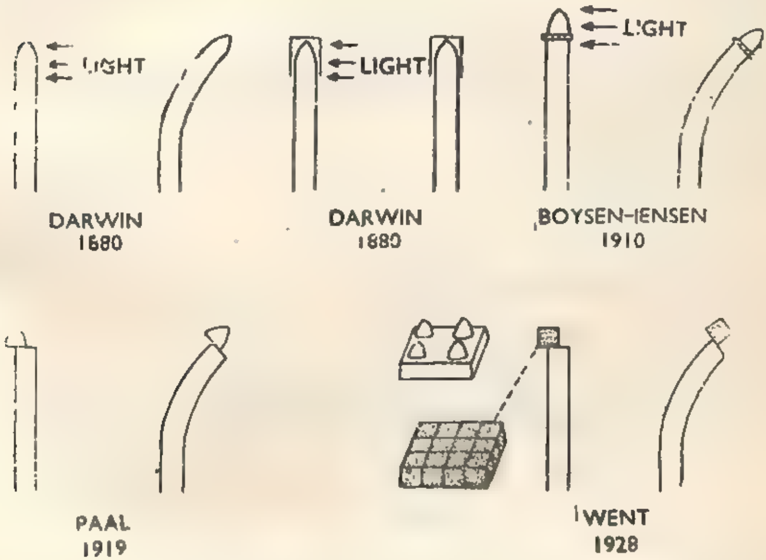


Fig. 86. Diagrammatic summary of the major steps in the discovery of the auxins.

F. W. Went (1926, 1928) was successful in isolating this growth substance from *Avena* coleoptile tips which still retained the growth promoting activity. He cut off the tips of the *Avena* coleoptiles and placed them on small agar-blocks for certain period of time and then placed the agar-blocks asymmetrically on cut coleoptile stumps. All the coleoptiles showed typical curvature even in dark. He also developed a method for determining the amount of this growth substance (*i.e.*, auxin) which is active in very small amounts in the *Avena* coleoptile tips. This method or the bioassay is famous by the name of *Avena* **Curvature Test**.

He concluded from this test that the curvature of the coleoptile is proportional within the limits of statistical error to the number of tips used and the length of time during which they remained on agar-blocks, or in other words, the curvature is proportional to the concentration of the active growth substance (*i.e.*, auxin) in agar-block.

Due to extremely small amount of this growth substance in the *Avena* coleoptile tips and lack of accurate methods of separating the constituents of the cell, it could not be possible to chemically analyse

this growth substance at that time. This probably led to the exploration of other sources, chief of which are human urine, *Rihzopus* cultures, malt and corn-grain oil.

Kogl and Haagen Smit (1931) isolated an active substance from human urine which was called as **Auxin-A** (or Auxen triolic

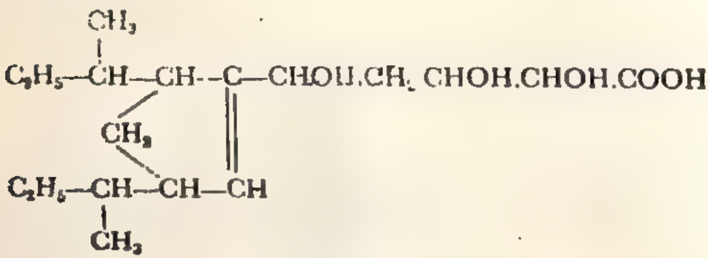


Fig. 87. Auxin—A (Auxentriolic acid).

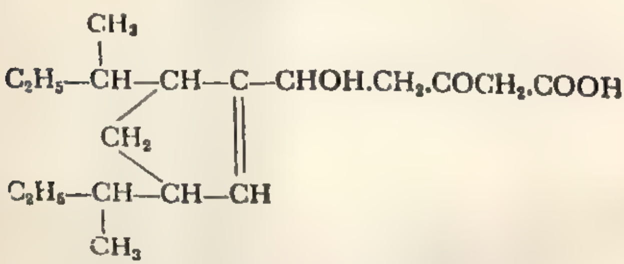


Fig. 88. Auxin—B (Auxenolonic acid)

acid). Later on in 1934, a similar active substance was isolated from malt and corn-grain oil and was named as **Auxin-B** (or Auxenolonic acid). Neither of these two auxins has ever been isolated again and there is considerable doubt regarding their existence.

Re-examination of human urine by Kogl *et al* (1934) and exmina-

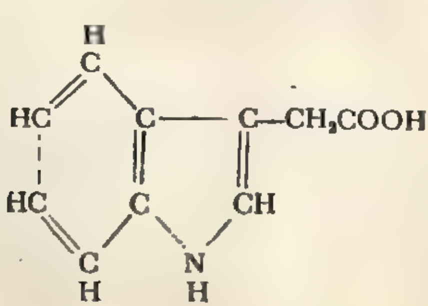
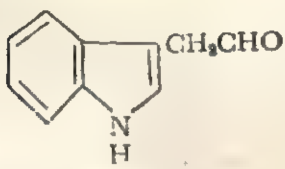


Fig. 89. Indole-3-acetic acid (IAA).

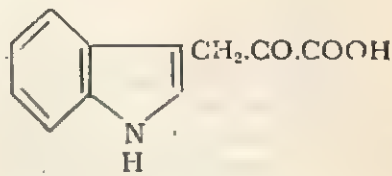
tion of *Rhizopus* Culture by **Thimann** (1935) led to the isolation of a different substance which was named as **Heteroauxin** (or other auxin). It appeared to be identical with an earlier known chemical compound called **Indole 3 Acetic Acid** (**IAA**).

Indole-3-acetic acid (IAA) has now been identified in a great variety of higher plants including the *Avena* coleoptile by using chromatographic, chemical and colourimeteric methods, and is considered to be the only **true natural auxin** of the higher plants.

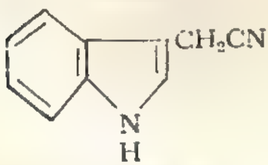
Some derivatives of Indole-3-acetic acid have also been detected from various plants which also exhibit auxin-like activity probably after their conversion into **IAA** *in vivo*. They are : Indole-3-acetaldehyde, Indole-3-pyruvic acid, Indole-3-acetonitrile and Indole-3-ethanol. Chemical structures of these derivatives are given below :



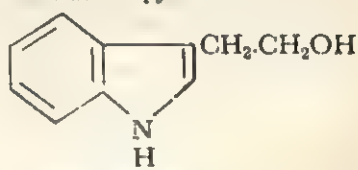
Indole-3-acetaldehyde



Indole-3-pyruvic acid



Indole-3-acetonitrile



Indole-3-ethanol

PHYSIOLOGICAL EFFECTS OF AUXIN

(1) Cell Elongation :

The primary physiological effect of auxin in plants is to stimulate the **elongation of cells in shoot**. A very common example of this can be observed in phototropic curvatures where the unilateral light unequally distributes the auxin in the stem tip (*i.e.*, more auxin on shaded side than on illuminated side). The higher concentration of auxin on the shaded side causes the cells on that side to elongate more rapidly resulting in bending of the stem tip towards the unilateral light.

Many theories have been proposed to explain the mechanism of cell elongation due to auxin. Accordingly, the auxin causes cell elongation probably :

(*i*) by increasing the osmotic solutes of the cells, or

(*ii*) by reducing the wall pressure, or

(*iii*) by increasing the permeability of cells to water, or

(*iv*) by an increase in the wall synthesis or

(*v*) by inducing the synthesis of specific **DNA** dependent new **m-RNA** and a specific enzymic protein. The latter bringing about an increase in cell plasticity and extension resulting ultimately in cell enlargement.

DNA → *m*RNA → Ribosome RNA → Synthesis of enzymes acting on cell wall. → Cell enlargement

t-RNA

Inhibited by Actinomycin D

Inhibited by Puromycin, Chloramphenicol etc.

Inhibited by high external osmotic pressure.

(2) Apical Dominance :

It has been a common observation in many vascular plants especially the tall and sparsely branched ones that if the terminal bud is intact and growing, the growth of the lateral buds just below it remained suppressed. Removal of the apical bud results in the rapid growth of the lataral buds. This phenomenon in which the apical bud dominates over the lateral buds and does not allow the latter to grow is called as **apical dominance**.

Skoog and Thimann (1934) first pointed out that the apical dominance might be under the control of auxin produced at the terminal bud and which is transported downward through the stem to the lateral buds and hinders their growth. They removed the apical bud of broad bean plant and replaced it with agar block. This resulted in rapid growth of lateral buds. But, when they replaced the apical bud with agar block containing auxin, the lateral buds remained suppressed and did not grow.

(3) Root Initiation :

In contrast to the stem, the higher concentration of auxin inhibits the elongation of roots but the number of lateral branch roots is considerably increased *i.e.*, the higher conc. of auxin initiates more lateral branch roots.

Application of **IAA** in lanolin* paste to the cut end of a young stem results in an early and extensive rooting. This fact is of great practical importance and has been widely utilized to promote root formation in economically useful plants which are propagated by cuttings.

*Lanolin is a soft fat prepared from wool and is a good solvent for auxins.

(4) **Prevention of Abscission :**

Natural auxins have controlling influence on the abscission of leaves, fruits etc.

(5) **Parthenocarpy :**

Auxin can induce the formation of parthenocarpic fruits. In nature also, this phenomenon is not uncommon and in such cases the concentration of auxins in the ovaries has been found to be higher than in the ovaries of plants which produce fruits only after fertilization. In the latter cases, the concentration of the auxin in ovaries increases after pollination and fertilization.

(6) **Respiration :**

It has been established that the auxin stimulates respiration and there is a correlation between auxin induced growth and an increased respiration rate. According to **French and Beevers** (1953) the auxin may increase the rate of respiration indirectly through increased supply of **ADP** (Adenosine diphosphate) by rapidly utilizing the **ATP** in the expanding cells.

(7) **Callus Formation :**

Besides cell elongation, the auxin may also be active in cell division. In fact, in many tissue cultures where the callus* growth is quite normal, the continued growth of such callus takes place only after the addition of auxin.

II. GIBBERELLINS
DISCOVERY AND CHEMICAL NATURE

The discovery of gibberellins is quite fascinating and dates back to about the same period when auxins were discovered, but it was only after 1950s that they came into prominence.

A young Japanese scientist **Kurosawa** had been trying to find out why the rice seedlings infected by the fungus *Gibberella fujikuroi* (asexual stage *Fusarium monoliforme*) grew taller and turned very thin and pale. These are the symptoms of 'Backanae disease' (meaning foolish) which is known to Japanese for over a century. In 1926, he succeeded in obtaining a filtered extract of this fungus which could cause symptoms of the Backanae disease in healthy rice seedlings. In 1935 **Yabuta** isolated the active substance which was quite heat stable and gave it the name **Gibberellin.**

Yabuta and Sumiki (1938) isolated gibberellin in crystalline form and identified **Gibberellin-A** and **Gibberellin-B** from their original preparation. In fact, these were the mixtures of different gibberellins which could not be separated at that time due to lack of suitable techniques. Later work showed that gibberellin-A was

*An undifferentiated mass of cells is called as callus.

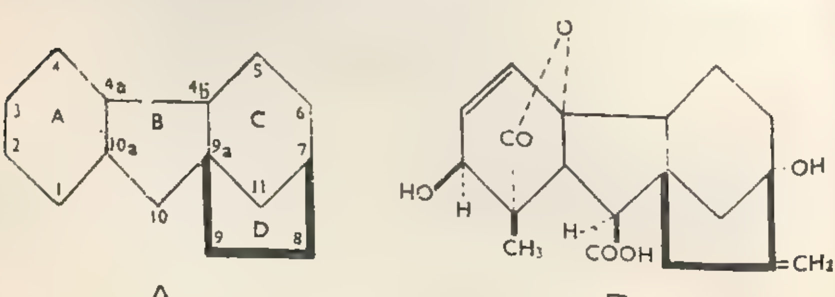
probably a mixture of 3 biologically active and gibberellin-B a mixture of one biologically active and one inactive gibberellins. The biological activity of gibberellins and their effect on different developmental processes of the plants were also studied by Japanese workers and published.

But, the European and American scientists did not give due importance to this work probably because (i) most of the scientists working on growth hormones were swayed by the impact of Indole-Acetic Acid (auxin) and other synthetic growth substances and (ii) English translations of the Japanese work were not available to them until after Second World War.

It was only in 1950 when **Mitchell** at the Biological Warfare Centre in U.S.A. and **Stodola** (1955) at the U.S. Dept. of Agriculture were engaged along with team of workers to isolate this substance on a commercial basis, that the importance of gibberellins was realised by western scientists. In England, **Brian** *et al* (1955) at the Imperial Chemical Laboratories independently obtained pure sample of a single gibberellin which was named as **gibberellic acid**. Later on, its structure was established by **Cross** *et al* (1961).

That there are different types of gibberellins had already been indicated by the work of **Yabuta and Sumiki**. It is now known that there are over 50 different gibberellins which have been isolated and chemically characterized.

All the gibberellins have a common skeleton the **gibbane-ring** (Fig. 90 A). They differ only in minute details viz., the number and position of—OH and sometimes—CH_3 and —COOH groups at different C atoms of gibbane-ring. Different gibberellins are named as GA_1, GA_2, GA_3, GA_4......GA_{29} and so on. GA_3 is called as gibberellic acid (Fig. 90 B) which is widely used by the scientists to show growth promoting properties of gibberellins.



A B

Fig. 90. A, Gibbane ring.
B, Structure of gibberellic acid (GA_3)

Apart from the fungal source, the gibberellins have now been isolated from wide variety of higher plants and are considered as natural plant growth hormones.

PHYSIOLOGICAL EFFECTS OF GIBBERELLINS

(1) Seed Germination

Certain **light sensitive seeds** *e.g.*, Lettuce and Tobacco show poor germination in dark. Germination starts vigourously if these seeds are exposed to light or red light. This requirement of light is overcome if the seeds are treated with gibberellic acid in dark.

(2) Dormancy of Buds

In temperate regions the buds formed in autumn remain dormant until next spring due to severe colds. This dormancy of buds can be broken by gibberellin treatment.

In potatoes also, there is a dormant period after harvest, but the application of gibberellin sprouts the eyes vigorously.

(3) Root Growth

Gibberellins have little or no effect on root growth. At higher concentration in some plants, however, some inhibition of root growth may occur. The initiation of roots is markedly inhibited by gibberellins in isolated cuttings.

(4) Elongation of the Internodes

Most pronounced effect of gibberellins on the plant growth is the elongation of the internodes, so much so that in many plants such as **dwarf pea**, **dwarf maize** etc., they overcome the **genetic dwarfism**. For instance, the light grown dwarf pea plants have short internodes and expanded leaves. But, when treated with gibberellin the internodes elongate markedly and they look like tall plants.

It is considered that in such dwarf plants (i) the gene for producing gibberellin is missing, or (ii) the concentration of the natural inhibitors is higher. When external gibberellin is applied the deficiency of the endogenous gibberellins is made good or the external gibberellin overcomes the effect of natural inhibitors which fall short.

(5) Bolting and Flowering

In many herbaceous plants the early period of growth shows **rosette-habit** with short stem and cauline leaves. Under short days this rosette habit is retained while under long days bolting occurs *i.e.*, the stem elongates rapidly and is converted into floral axis bearing flower primordia. This bolting can also be induced in such plants *e.g. Rudbeckia speciosa* (It is a Long Day Plant.*) by the application of gibberellin even under non-inductive short days.

*For details see Chapter 18

In *Hyoscyamus niger* (also a Long Day Plant) gibberellin treatment causes bolting and flowering under non-inductive short days. While in Long Day Plants the gibberellin treatment usually results in early flowering, its effects are quite variable in Short Day Plants. It may either have no effect, or inhibit, or may activate flowering.

(6) Parthenocarpy

Germination of the pollen grains is stimulated by gibberellins, likewise the growth of the fruit and the formation of parthenocarpic fruits can be induced by gibberellin treatment. In many cases *e.g.*, pome and stone fruits where auxins have failed to induced parthenocarpy the gibberellins have proven to be successful. Seedless and fleshy tomatoes and large sized grapes are produced by gibberellin treatment on commercial scale..

(7) Light Inhibited Stem Growth

It is a common observation that the dark grown plants become etiolated and have taller, thinner and pale stems while the light grown plants have shorter, thicker and green stems, and it may be concludedthat light has inhibitory effect on stem elongation. Treatment of light grown plants with gibberellin also stimulates the stem growth and they appear to be dark grown. In such cases the protein content of the stem falls while soluble nitrogen content increases probably due to more breakdown of proteins than their synthesis.

It is considered that the light in some way lowers the level of endogenous gibberellins and inhibits the stem growth.

(8) *de novo* **Synthesis of the Enzyme-*α-Amylase*.**

One of the important functions of gibberellins is to cause *de novo** synthesis of the enzyme *amylase* in the **aleurone layer** of the endosperm of cereal grains during germination. This enzyme brings about hydrolysis of starch to form simple sugars which are then translocated to growing embryo to provide energy source.

III. KINETIN AND CYTOKININS
DISCOVERY AND CHEMICAL NATURE

The discovery of Kinetin is comparatively more recent. Its credit goes to **Miller** *et al* (1950) who were working in Prof. **Skoog's** lab. at the University of Wisconsin on the growth of tobacco pith callus in culture and wanted it to grow indefinitely. They added various **growth substances**, nutrients, *vitamins* etc. into the culture medium but failed till they noticed an old bottle of **DNA** kept for several years in their lab. They added the contents of that bottle to the culture medium and observed that the tobacco pith callus could grow for longer periods. They obtained similar results with *Yeast* extract.

**de novo*=a new.

But, they did not get positive results with fresh **DNA** and thought the active substance to be some **degradation product of DNA**. They isolated this substance by autoclaying (heating under pressure) the **DNA** which had been stored for long. It could easily be precipitated by silver salts and was soluble in 90% alcohol, indicating that possibly it was a **purine compound**. Later on, they identified it as **6-furfurylaminopurine**. Because of its specific effect on **cytokinesis** *i.e.*, cell division, it was called as **kinetin** (Fig. 91).

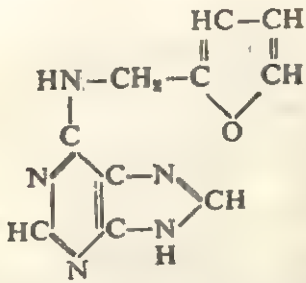


Fig. 91. Structure of Kinetin (6-furfurylaminopurine).

Although kinetin has profound influence in inducing cell division, still it has not been isolated from any plant. But, certain substances which show kinetin like activity have in fact been isolated from a variety of higher plants. These substances are collectively called as **cytokinins**. There is now sufficient evidence to show that cytokinins do occur in plants and regulate growth and hence, they are also considered as **natural plant growth hormones**.

Some of the very important and commonly known naturally occurring cytokinins are as follow :

(i) COCONUT MILK FACTOR

The liquid endosperm of coconut (*Cocos nucifera*) often referred to as coconut milk has been found to contain some factors which show kinetin like activity and can stimulate growth in many plant tissues *in vitro*. Although a number of purine compounds showing kinetin like activity have been isolated from coconut milk, but attempts to isolate and identify the active ingredients of coconut milk by various workers are still continuing.

In many plant tissues *e.g.*, secondary phloem from the root of *Daucus carota* and mesocarp from the fruit of *Prunus persica*, if auxin is also supplied in the medium the coconut milk shows so much kinetin like activity that it can replace the latter.

(ii) ZEATIN

Although this cytokinin was known earlier but it was obtained in pure crystalline form in 1963 by **Letham** from immature corn grains and named as zeatin (Fig. 151). It was identified as **6-(4 hydroxy**

3-methylbut-trans-2-enyl) aminopurine by **Letham** *et al* (1964) and was synthesized by **Shaw and Wilson** (1964).

Zeatin is remarkably more active than any other known cytokinin probably because of the presence of a highly reactive **allylic –OH** group in its side chain. The existing reports do not rule out the possibility that this cytokinin is widely distributed in the plant kingdom.

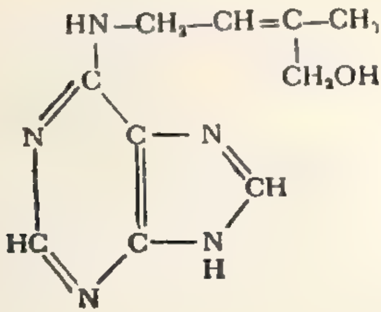


Fig. 92.. Structure of Zeatin

CYTOKININS IN t-RNA

In 1966 **Zachau et al** identified a cytokinin **2iPA*** as a constituent of two serine t-RNA species from brewers yeast and showed this cytokinin to be adjacent to the **3′ end** of the anticodon in both the species.

Apart from yeast, cytokinins have now been found in t-RNA preparations from a wide variety of organisms such as bacteria including *E. coli*, animals including man and higher plants *viz.*, corn seedlings, immature corn kernels, frozen peas, tobacco callus tissue and wheat germ.

It has been suggested by various workers that the association of a particular cytokinin with anticodon of the t-RNA molecule might have a bearing on codon-anticodon interaction between t-RNA and m-RNA during protein synthesis. For instance, in case of yeast serine t-RNA the chemical modification of the cytokinin (associated with the latter) had no effect on the acceptance of serine by the t-RNA but interfered with the subsequent binding of the charged t-RNA to the m-RNA-Ribosomal complex.

* Chemical name of this cytokinin is 6-(3-Methyl-2-butenylamino)-9-3-D-ribofuranosylpurine.

PHYSIOLOGICAL EFFECTS OF KINETIN (CYTOKININS)

(1) Cell Division

One of the most important biological effects of kinetin on plants is to induce cell division in the presence of sufficient amount of auxin **(IAA)**, especially in tobacco pith callus, carrot root tissue, soyabean cotyledon, pea callus etc.

(2) Cell Enlargement

Like auxins and gibberellins, the kinetin may also induce cell enlargement. Significant cell enlargement has been observed after kinetin treatment in leaf discs cut from etiolated leaves of *Phaseolus vulgaris*, pumpkin cotyledones, tobacco pith cultures, cortical cells of tobacco roots, excised Jerusalem artichoke tissues etc.

(3) Initiation of Interfascicular Cambium

Kinetin can induce formation of interfascicular cambium. This has in fact been shown by **Sorokin** *et al* (1962) in pea stem sections.

(4) Morphogenesis

Kinetin also has ability to cause morphogenetic changes in an otherwise undifferentiated callus. For instance, the tobacco pith callus can be made to develop either buds or roots by changing the concentration of kinetin and auxin :

High Auxin
+ → Roots
Low Kinetin

Low Auxin
+ → Buds
High Kinetin

The effect of kinetin in stimulating or initiating the formation of buds has also been observed in leaf cuttings of *Saintipaulia ionantha*, *Begonia*, *Bryophyllum* and in mosses *e.g.*, *Tortella* etc.

A positive effect of kinetin on the regeneration of shoots from cultured root segments has also been reported in *Isatis tinctoria* and *Convolvulus arvensis*.

(5) Counteraction of Apical Dominance

Wickson and **Thimann** (1958) in one of their experiments found that the growth of the lateral buds of pea stem section (second internode) in culture solutions containing **IAA** was inhibi-

ted. But the growth of lateral buds could continue if **IAA** was not included. On the other hand, the addition of kinetin along with **IAA** stimulated the growth of these buds. They obtained similar results with entire shoots and concluded that the apical dominance might be under the control of a balance of concentrations between endogenous kinetin like substances (cytokinins) and **IAA**.

(6) Dormancy of Seeds

Like gibberellins, the dormancy of certain light sensitive seeds such as lettuce and tobacco can also be broken by kinetin treatment in dark. Furthermore, the inhibitory effect of far-red light treatment on the germination of the above seeds is also overcome by kinetin treatment.

Seeds of parasitic plants *e.g.*, *Striga asiatica* which require the presence of their host for germination can also be induced to germinate by treating them with kinetin even in the absence of their host.

(7) Delay of Senescence : The Richmond-Lang Effect

The ageing process of the leaves usually accompanies with loss of chlorophyll (*i.e.*, yellowing) and rapid breakdown of proteins. This is called as **senescence**. In 1957, **Richmond** and **Lang** showed that this senescence could be postponed to several days in detached *Xanthium* leaves by kinetin treatment. This effect of kinetin in delaying the senescence is called as **Richmond-Lang effect**.

Mothes (1960) and other workers have shown mobilization of nutrients and other substances including auxins to the kinetin treated areas. In intact plants, the delay of senescence at some part due to kinetin treatment may result in senescence in other parts of the plant.

The observations of **Osborne** (1962) and other workers suggest that the high protein content in kinetin treated tissue is probably due to more synthesis of proteins than their degradation, and this in turn may be due to the regulatory action of kinetin on **RNA** synthesis.

One of the important factors in delay of senescence in kinetin treated leaves is their physiological age. For instance, mature leaves of *Tobacco rustica* have been found to be more responsive to kinetin treatment in delaying senescence than the younger leaves.

OTHER NATURAL GROWTH HORMONES IN PLANTS

Ethylene ($CH_2 = CH_2$)

The effect of ethylene in hastening the colouring of harvested lemons and the post harvest maturation of many fruits *e.g.*,

bananas, pears, apples, tomatoes etc., has been known for about 60 years. It was also known that most fruits, flowers, leaves of certain plants and certain fungi viz., *Penicillium digitatum*, *Alternaria citri* and *Blastomyces dermatitidis* produce small amounts of ethylene but the recognition of ethylene as a **natural plant growth hormone** was done only recently (**Pratt** and **Goeschl** 1969).

Important Physiological Effects

- It hastens post harvest maturation of fruits *e.g.*, bananas, pears, apples, tomatoes, citrus fruits etc.

- It is effective in inducing flowering in pineapple plants.

- Small amount of ethylene in air causes a triple response in some plants which consists of (*i*) epinasty of the leaves (*ii*) swelling of the stems, and (*iii*) inhibition of extensive growth.

- Induces or stimulates root formation in some plants.

- In certain plants it causes abnormal growth of axillary buds and accelerates leaf abscission.

- It increases the rate of respiration of potatoes and inhibits the sprouting of potatoes.

Traumatic Acid (Wound Hormone)

The phenomenon of callus formation on injury in plants is a common observation. **Haberlandt** (1913) postulated that the injured cells release a '**wound hormone**' which causes the adjacent uninjured cells to become meristematic and divide till the wound is healed up.

English *et al* (1939) isolated and identified the active substance as **traumatic acid**. The structure of the traumatic acid which is a straight-chain unsaturated dicarboxylic acid is given below :

$$COOH-CH=CH-(CH_2)_8-COOH$$

It requires glutamic acid, sucrose and phosphate as cofactors for its activity to form the callus.

Although traumatic acid has been found to be very active in inducing meristematic activity in uninjured green bean pods, but it is not effective in most of the plant tissues including tobacco pith tissue.

Calines (Formative Hormones)

In recent years indirect evidences have persuaded some workers to postulate the existence of certain other natural growth hormones in plants called as **calines** or **formative hormones**

which are throght to be essential for the effect of auxin on root, stem and leaf growth. They are :—

(i) **Rhizocaline or Root Forming Hormone.** It is produced by the leaves and translocated in a polar manner down the stem.

(ii) **Caulocaline or Stem Forming Hormone.** It is produced by the roots and is transported upward in the stem.

(iii) **Phyllocaline or Leaf Forming Hormone.** It is produced probaby by the cotyledones It stimulates mesophyll development in the leaves and is synthesized only in the presence of light.

None of these calines has yet been isolated.

13

Photoperiodism

PHOTOPERIODISM

The plants in order to flower require a certain day length *i.e.*, the relative length of day and night which is called as **photoperiod**. The response of plants to the photoperiod expressed in the form of flowering is called as **photoperiodism**.

The phenomenon of photoperiodism was first discovered by **Garner** and **Allard** (1920, 22) who observed that the Biloxi variety of Soyabeans (*Glycine max*) and 'Maryland Mammoth' variety of tobacco (*Nicotiana tabaccum*) could be made to flower only when the daily exposure to the light was reduced below a certain critical duration and after many complex experiments concluded that 'the relative length of the day is a factor of the first importance in the growth and development of plants'.

Depending upon the duration of the photoperiod, they classified plants into three categories :

(1) SHORT DAY PLANTS (SDP)

These plants require a relatively short day light period (usually 8-10 hours) and a continuous dark period of about 14-16 hours for subsequent flowering (Fig. 93 A). Some examples of these plants which are also known as **long-night-plants** are Maryland Mammoth variety of tobacco (*Nicotiana tabaccum*) Biloxi variety of Soyabeans (*Glycine max*), Cocklebur (*Xanthium pennsylvanicum*).

● In short day plants the dark period is critical and must be continuous. If this dark period is interrupted even with a brief exposure of red light (660-665 mμ wavelength), the short day plant will not flower (Fig 93 B).

● Maximum inhibition of flower with red light occurs at about the middle of critical dark period.

- However, the inhibitory effect of red light can be overcome by a subsequent exposure with far-red light (730-735 mμ wavelength).
- Interruption of the light period with red light does not have inhibitory effect on flowering in short day plants (Fig. 93 C).
- Prolongation of the continuous dark period initiates early flowering in short day plants.

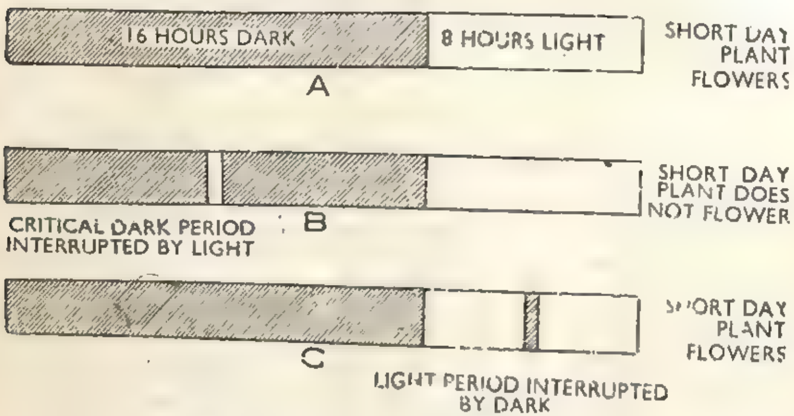


Fig. 93 . Effect of a brief exposure of red light during dark and light periods on flowering in a short day plant.

(2) LONG DAY PLANTS (LDP)

These plants require a longer day light period (usually 14-16 hours) in a 24 hours cycle for subsequent flowering. Some examples of these plants which are also called as **short night plants** are *Hyoscyamus niger* (Henbane), *Spinacea* (spinach) *Beta vulgaris* (Sugar beet).

- In long day plants the light period is critical.
- A brief exposure in the dark period or the prolongation of the light period stimulates flowering in long day plants.

(3) DAY NEUTRAL PLANTS

These plants flower in all photoperiods ranging from 5 hours to 24 hours continuous exposure. Some of the examples of these plants are tomato, cotton, sunflower cucumber and certain varieties of peas and tobacco.

During recent years certain intermediate categories of plants have also been recognised. They are,

Long Short Day Plants

These are short day plants but must be exposed to long days

during eary periods of growth for subsequent flowering. Some of the examples of these plants are certain species of *Bryophyllum*.

Short-Long Day Plants

These are long day plants but must be exposed to short days during early periods of growth for subsequent flowering. Some of the examples of these plants are certain varieties of wheat (*Triticum*) and rye (*Secale*).

PHOTOPERIODIC INDUCTION

Plants may require one or more **inductive cycles** for flowering. An appropriate photoperiod in a 24 hours cycle constitutes one inductive cycle. If a plant which has received sufficient inductive cycles is subsequently placed under unfavouarble photoperiods, will still flower. Flowering will also occur if a plant receives inductive cycles after intervals of unfavourable photoperiods (*i.e.*, discontinuous inductive cycles). This persistence of photoperiodic after effect is called as **photoperiodic induction**.

- An increase in the number of inductive cycles results in early flowering of the plant. For instance, *Xanthium* (a short day plant) requires only one inductive cycle and normally flowers after about 64 days. It can be made to flower even after 13 days if it has received 4-8 inductive cycles. In such cases the number of flowers is also increased.

- Continuous inductive cycles promote early flowering than discontinuous inductive cycles.

Some of the examples of plants which require more than one inductive cycles for subsequent flowering are Biloxi soyabean (SDP)—2 inductive cycles; *Salvia occidentalis* (SDP)—17 inductive cycles; *Plantago lenceolata* (LDP)—25 inductive cycles.

PERCEPTION OF THE PHOTOPERIODIC STIMULUS AND PRESENCE OF A FLORAL HORMONE

It is now well established that the photoperiodic stimulus is perceived by the leaves. As a result, a floral hormone is produced in the leaves which is then translocated to the apical tip, subesquently causing the initiation of floral primordia.

That the photoperiodic stimulus is perceived by the leaves can be shown by simple experiments on cocklebur (*Xanthium pennsylvanicum*), a short day plant. Cocklebur plant will flower if it has previously been kept under short-day conditions (Fig. 94 A). If the plant is defoliated and then kept under short day condition, it will not flower (Fig. 94 B). Flowering will also occur even if all the leaves of the plant except one leaf have been removed (Fig. 94 C).

If a cocklebur plant whether intact or defoliated, is kept under long day conditions it will not flower (Fig. 94 D, E). But, If even one of its leaves is exposed to short day condition and the rest are under long day photoperiods, flowering will occur (Fig. 94 F).

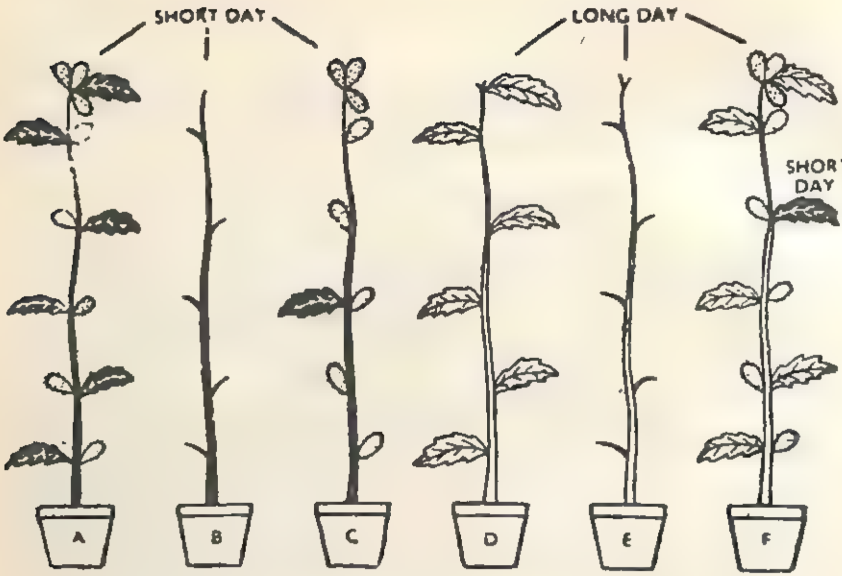


Fig. 94. Experiment on cocklebur plants to show that photoperiodic stimulus is perceived by the leaves. Flowering occur even if a single leaf is exposed to appropriate photoperiod. See text

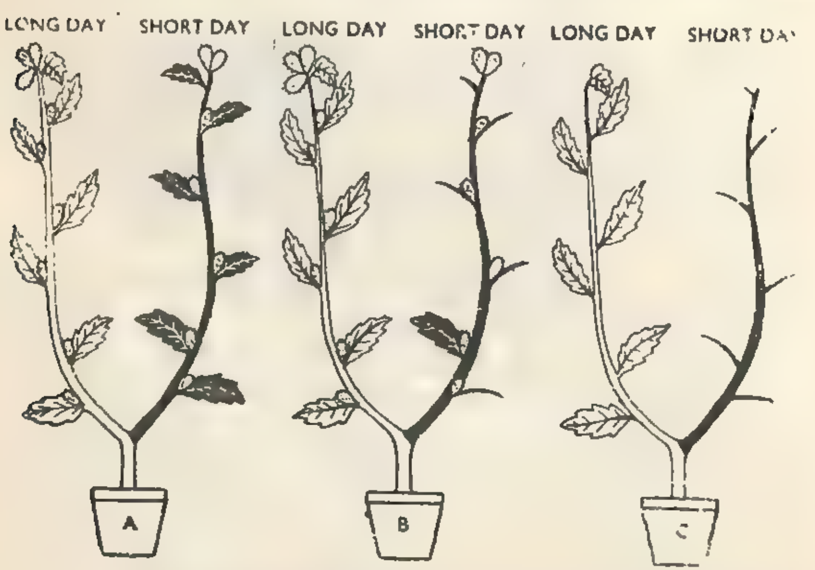


Fig. 95. Experiments on cocklebur plants to show that the photoperiodic stimulus can be transmitted from one branch of the plant to another.

The photoperiodic stimulus can be transmitted from one branch of the plant to another branch. For example, if in a two branched cocklebur plant one branch is exposed to short day and other to long day photoperiods, flowering occurs on both the branches (Fig. 95 A) Flowering also occurs if one branch is kept under long day conditions and other branch from which all the leaves except one have been removed is exposed to short day condition (Fig. 95 B). However, if one branch is exposed to long photoperiod and the other has been defoliated, under short day condition, flowering will not occur in any of the branches (Fig. 95 C).

Nature of the Floral Hormone

Although there are firm evidences for the existence of a floral hormone but is has not yet been isolated. Therefore, the nature of this hormone which has been named as **florigen** is not very clear. But it is quite evident that this hormone is a **material substance** which can be translocated from leaves to the apical tips situated at other parts of the plant resulting in flowering.

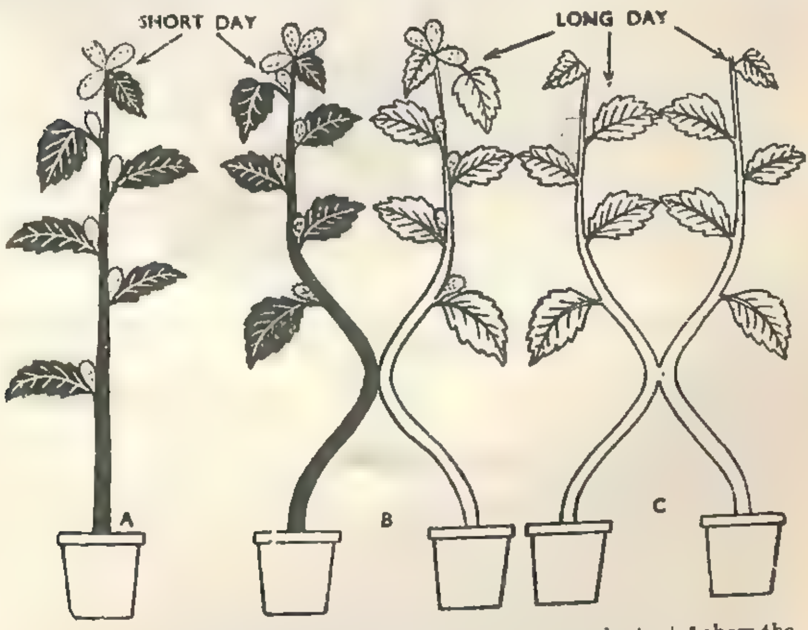


Fig. 961. Grafting experiments in cocklebur plants to show the translocation of floral hormone from one plant to another through graft union.

Grafting experiments in cocklebur plants have even proved that the floral hormone can be translocated from one plant to another. For example, if one branched cocklebur plant (Fig. 96. A) which has been exposed to short day conditions is grafted to another cocklbur plant kept under long day conditions, flowering occur on both the plants (Fig 96 B). Obviously the floral hormone has been

transmitted to the receptor plant through graft union. But if a cocklebur plant is grafted to another similar plant both of which have been kept under long day conditions, flowering will not occur on either of the two plants (Fig. 96 C).

It has also been indicated that the floral hormone may be identical in short-day and long-day plants. For example, grafting experiments between certain long-day plant and short day plants have shown that flowering occurs on both the plants even if one of them has beon kept under non-inductive photoperiods.

PHYTOCHROME

It has already been seen that a brief exposure with red light during critical dark period inhibits flowering in short-day plants and this inhibitory effect can be reversed by a subsequent exposure with far-red light. Similarly, the prolongation of the critical light period or the interruption of the dark period stimulates flowering in long-day plants. This inhibition of flowering in short-day plants and the stimulation of flowering in long-day plants involves the operation of a proteinaceous pigment called as **phytochrome.**

- The pigment phytochrome exists in two different forms, (*i*) red light absorbing form which is designated as $\mathbf{P_R}$ and (*ii*) far-red light absorbing form which is designated as $\mathbf{P_{FR}}$.
- These two forms of the pigment are photochemically interconvertible.
- When $\mathbf{P_R}$ form of the pigment absorbs red light (660-665 mμ) it is converted into $\mathbf{P_{FR}}$ form.
- When $\mathbf{P_{FR}}$ form of the pigment absorbs far-red light (730-735 mμ), it is converted into $\mathbf{P_R}$ form.
- The $\mathbf{P_{FR}}$ form of the pigment gradually changes into $\mathbf{P_R}$ form in dark.

$$\begin{tikzcd} P_R \arrow[r, shift left, "660\text{-}665\ m\mu"] & P_{FR} \arrow[l, shift left, "730\text{-}735\ m\mu"] \arrow[l, bend left=60, dotted, "\text{Darkness}"] \end{tikzcd}$$

It is considered that during the day the $\mathbf{P_{FR}}$ form of the pigment is accumulated in the plant which is inhibitory to flowering in short-day plants but is stimulatory in long-day plants. During critical dark period in short-day plants, this form gradually changes into $\mathbf{P_R}$ form resulting in flowering. A brief exposure with red light will convert this form again into $\mathbf{P_{FR}}$ form thus inhibiting flowering. Reversal of the inhibitory effect of red light during critical dark period in SDP by subsequent far-red light exposure is because the $\mathbf{P_{FR}}$ form after absorbing far-red light (730-735 mμ) will again be converted back into $\mathbf{P_R}$ form.

Prolongation of the critical light period or the interruption of the dark period by red-light in long-day plants will result in further accumulation of the P_{FR} form of the pigment, thus stimulating flowering in long-day plants.

GIBBERELLINS AND THE FLOWERING RESPONSE

It is now well known that the gibberellins can induce flowering in long-day plants even under non-inductive short days. It is also definite that the gibberellins alone do not constitue the 'florigen'. but it is usually held that the gibberellins are in some way connected with the overall process of flowering.

According to a scheme proposed by **Brian** (1958) a gibberellin like hormone is produced in the leaves during the photoperiod somewhat as follows :

$$CO_2 \rightarrow \text{Precursor (P)} \rightarrow \text{Gibberellin-like hormone}$$

The precursor may be slightly stimulatory or inactive or antagonistic to the gibberellin-like hormone. Red irradiations promote the conversion of the precursor to the gibberellin-like hormone. In the dark there is a slow reconversion of the gibberellin-like hormone to the precursor. This reconversion is accelerated by far-red irradiations. It is further presumed that high concentration of the gibberellin-like hormone leads to the synthesis of florigen in long-day plants. In short day plants the synthesis of florigen takes place when the level of gibberellin-like hormone is low. But, flowering eventually follows once the florigen synthesis has taken place in both the cases. The whole scheme is diagrammatically shown below :

$$CO_2 \rightarrow \text{Precursor} \underset{\text{Far-red}}{\overset{\text{Red}}{\rightleftarrows}} \text{Gibberellin-like hormone} \rightarrow \text{Florigen}$$

Darkness

IMPORTANCE OF PHOTOPERIODISM

(*i*) The knowledge of the phenomenon of photoperiodism has been of great practical importance in hybridisation experiments.

(*ii*) Although the floral hormone 'florigen' has not yet been isolated, the isolation and characterization of this hormone will be of utmost economic importance.

(*iii*) The phenomenon of photoperiodism is an excellent example of **physiological preconditioning** (or after-effect) where an external factor (*i.e.*, the photoperiodic stimulus) induces some physiological changes in the plant the effect of which is not immediately visible. It lingers on in the plant and prepares the latter for a certain process (*i.e.*, flowering) which takes place at a considerably later stage during the life history of the plant.

14

Vernalization

VERNALIZATION

Besides an appropriate photoperiod certain plants require a low temperature treatment during their earlier stages of the life history for subsequent flowering in the later stages. This was first realised by **Klippart** in 1857 when he found that the **winter wheat** (sown in winter and flowering in summer) could be converted into **spring wheat** (sown in spring and flowering in summer) if the seeds after slight germination were kept at nearly freezing temperature (0° – 5°C). This conversion of the winter variety into the spring variety by low temperature or chilling treatment was termed as **vernalization** by **Lysenko** (1928). Due to vernalization the vegetative period of the plant is cut short resulting in an early flowering.

The phenomenon of vernalization was extended to many other plants by different workers like **Lysenko**, **Gessner** etc., and it was found that many winter annuals *e.g.*, Petkus winter rye (*Secale cereale*), some biennials *e.g.*, *Hyoscyamus niger* (Henbane*) and even certain perennials *e.g.*, apples have a low temperature requirement for subsequent flowering. However, certain plants such as Petkus winter rye do not have an absolute cold requirement for flowering In such cases the cold temperature only shortens the time to flower. Chouard (1960) has reviewed the work on vernalization in detail and defined it as "acquisition or acceleration of the ability to flower by a chilling treatment."

The effect of the cold stimulus on plant is not immediately visible. It is expressed only at a certain later stage in the form of flowering. Thus like the photoperiodism, the phenomenon of vernalization is an excellent example of the **physiological preconditioning**.

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* It has annual variety also. The biennial variety may be converted into annual variety by vernalizing the former during its early period of growth.

PERCEPTION OF THE COLD STIMULUS

The cold stimulus is perceived by the **apical meristems**. But the work of **Wellensiek** (1964) on the vernalization of the excised (or isolated) leaf and root of *Lunaria biennis* has shown that **all dividing cells** including those in roots or leaves may be the potential sites of vernalization.

(The plants regenerated from isolated leaves or roots of unvernalised *Lunaria biennis* plant require vernalization in order to flower. But if the isolated leaves or roots are given a chilling treatment for sufficient time, the plants regenerated from them respond as if they themselves have been vernalized).

PRESENCE OF A FLORAL HORMONE

It is believed that the perception of the cold stimulus results in the formation of a floral hormone which is transmitted to other parts of the plant. In certain cases the cold stimulus may even be transmitted to another plant across a graft union. For instance, if a vernalized henbane plant is grafted to an unvernalized henbane plant, the latter also flowers.

The above mentioned floral hormone has been named as **vernalin by Melchers** (1939) but it is yet to be isolated.

OTHER CONDITIONS NECESSARY FOR VERNALIZATION

(1) **Age of the plant**. The age of the plant is an important factor in determining the responsiveness of the plant to the cold stimulus and it differs in different species. For example, in cereals like winter wheat the vernalization is effective only if the germinating seeds have received a cold temperature treatment for sufficient time, while in case of biennial variety of henbane (*Hyoscyamus niger*) the plants will respond to the cold temperature treatment only if they are in rosette stage and have completed at least 10 days of growth.

(2) **Appropriate Low Temperature and Duration of the Exposure.** Most suitable temperature for vernalizing the plants ranges between 1—6°C. The effectiveness of the low temperature treatment decreases from 0°C to —4°C. Low temperature at about —6°C is completely ineffective. Similarly, at higher temperatures from 7°C onwards the response of the plants is decreased. Temperatures at about 12—14°C are almost ineffective in vernalizing the plants.

Besides an appropriate low temperature a suitable duration of this cold treatment is essential for vernalization. Depending upon the degree of low temperature and in different species this period may vary, but usually the duration of the chilling treatment is about one and a half months or more.

(3) **Oxygen.** The vernalization is an **aerobic process**, and requires metabolic energy. In absence of oxygen the cold treatment becomes completely ineffective.

(4) **Water.** Sufficient amount of water is also essential for vernalization. Vernalization of the dry seeds is not possible.

MECHANISM OF VERNALIZATION

The mechanism of vernalization is obscure. The two main hypothetical theories are given below :—

(1) Phasic Development Theory

The main points of this theory which was advanced by **Lysenko** (1934) are as follow :—

(*i*) The growth (increase in size) and development (*i.e.*, the progressive change in the characteristic of the new organs) are two distinct phenomena.

(*ii*) According to this theory the process of the development of an annual seed plant consists of a series of **phases** which must occur in some predetermined sequence.

(*iii*) Commencement of any of these phases will take place only when the preceding phase has been completed.

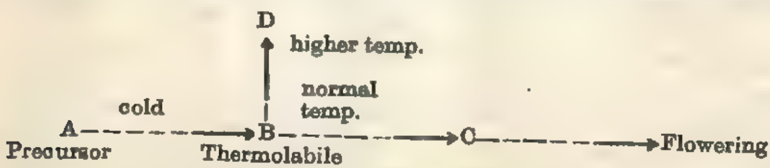
(*iv*) The phases require different external conditions for completion such as light and temperature.

(*v*) Vernalization accelerates the **thermophase** *i.e.*, that phase of development which is dependent upon temperature.

Thus, in winter wheat variety low temperature is required for the completion of the first thermophase. After this the next phase which is dependent upon light (photophase) starts. Vernalization of the winter wheat accelerates the first thermophase so that there is an early swing from vegetative to the reproductive phase or flowering.

(2) Hormonal Theories

It has already been described that vernalization probably involves the formation of a floral hormone called as vernalin. Based on this fact, many hypothetical schemes have been proposed by different workers from time to time. The first hormonal theory proposed by **Lang** and **Melchers** (1947) is schematically shown below :—



According to this scheme, the precursor A is converted into a thermolabile componnd **B** during cold treatment. Under normal conditions **B** changes into **C** which ultimately causes flowering. But at higher temperatures **B** is converted into **D** and flowering does not take place (devernalization)

DEVERNALIZATION

The positive effect of the low temperature treatment on the vernalization of the plants can be counteracted by subsequent high temperature treatment. This is called as **devernalization**. The degree of devernalization decreases if the duration of the cold treatment has been longer. However, the devernalized plant can again be vernalized by subsequent low temperature treatment.

VERNALIZATION AND GIBBERELLINS

The gibberellins are known to replace the low temperature requirement in certain biennial plants such as henbane, where the plant normally remains vegetative and retains its rosette habit during the first growing season and after passing through the winter period flowers in the next season. The gibberellins cause such plants to flower even during the first year.

It has been suggested that in such cases the gibberellins probably through stem elongation trigger some reactions leading to flowering.

PRACTICAL UTILITY OF VERNALIZATION

(*i*) Vernalization shortens the vegetative period of the plants.

(*ii*) Vernalization increases the cold resistance of the plants.

(*iii*) In colder countries like Russia, where the winters are too severe, vernalization has been of great importance in agriculture. By this process certain crop plants could be made to escape the harmful effects of severe winters, thus improving the crop production. In warmer countries like India, however, vernalization practice has not been in use mainly because it is a costly process and the winters are comparatively not very severe as to harm the crop plants. Moreover, the vernalization processes have resulted only in very little success in India.

(*iv*) Early work by Russians has also claimed that vernalization increases the resistance of plants to fungal diseases.

15

Dormancy of Seeds

DORMANCY OF SEEDS

All the viable seeds have capacity to germinate if placed under suitable conditions necessary for germination. While in certain plants such seeds will immediately germinate after harvest, in others they **fail to germinate for sometime** even if placed under such conditions that are ordinarily favourable for germination either due to some **internal factors** or due to specific requirement for some environmental factors. During this period the growth of the seeds remains **suspended** and they are said to be in **rest stage** or **dormant stage** and this phenomenon is called as **dormancy of seeds.**

FACTORS CAUSING DORMANCY OF SEEDS

Dormancy of seeds results from one or a combination of several different factors which are described below :

(1) Seed Coats Impermeble to Water

The seeds of certain plants especially those belonging to the families Leguminosae, Malvaceae, Chenopodiaceae, Convolvulaceae, and Solanaceae have very hard seed coats which are impermeable to water. The seeds remain dormant in the soil until the impermeable layer of testas decay by the action of soil micro-organisms.

(2) Seed Coats Impermeable to Oxygen

In many plants such as cocklebur (*Xanthium*), many grasses and some members of the family compositae the dormancy of seeds results from the impermeability of the seed coats to oxygen.

However, during the period of dormancy the seed coats gradually become more permeable to oxygen so that they may germinate afterwards.

(3) Mechanically Resistant Seed Coats

The seeds of certain weeds such as pigweed (*Amaranthus*), shepherd's purse (*Capsella*). water plantain (*Alisma*) etc., remain dormant because their hard seed-coats prevent any appreciable expansion of the embryo. This dormancy may persist up to periods as long as 30 years in case of pigweed if the seeds remain saturated with water. However, if the seed coats become dry and then again saturated with water, they are no longer able to resist the expansion of the embryo. The seed coats rupture aud germination takes place. At higher temperatures (above 40°C) also the seed coats in pigweed become less resistant to pressure developed by the imbibitional forces in the embryo so that some germination may take place.

(4) Immaturity of the Embryo

In many plants *e.g.*. certain orchids, *Ginkgo biloba*, *Anemone nemorosa*, *Fraxinus excelsior* etc. the seed dormancy results from the immaturity of the embryos which fail to develop fully by the time the seeds are shed. In such cases the seeds germinate only after a period of rest during which the development of embryo inside the seeds is completed.

(5) Need for After Ripening in Dry Storage

In many plants *e.g.*, barley, oats, wheat etc., the seeds though containing fully developed embryos are dormant when they are harvested. They require no special treatment to overcome this dormancy and germinate if kept under dry storage conditions at normal temperatures for about a few weeks to several months. During this period probably due to certain physiological changes in the embryo, the seeds develop the capacity to germinate which is called as after-ripening. The nature of these physiological changes during after -ripening is not clear.

The dormancy of the cereal seeds, however, may be removed either by storing them at 35 to 40°C for 2 to 4 days or removing their seed-coats.

(6) Germination Inhibitors

Sometimes, the dormancy of seeds results due to the presence of certain germination inhibitors either in some parts of the seeds such as testa, endosperm, embryo or in structures surrounding them such as the juice or the pulp of fruit (*e.g.*, in tomato) and glumes (*e.g.*, in oats). The molecular structures of some of the common natural germination inhibitors are given in Fig. 97.

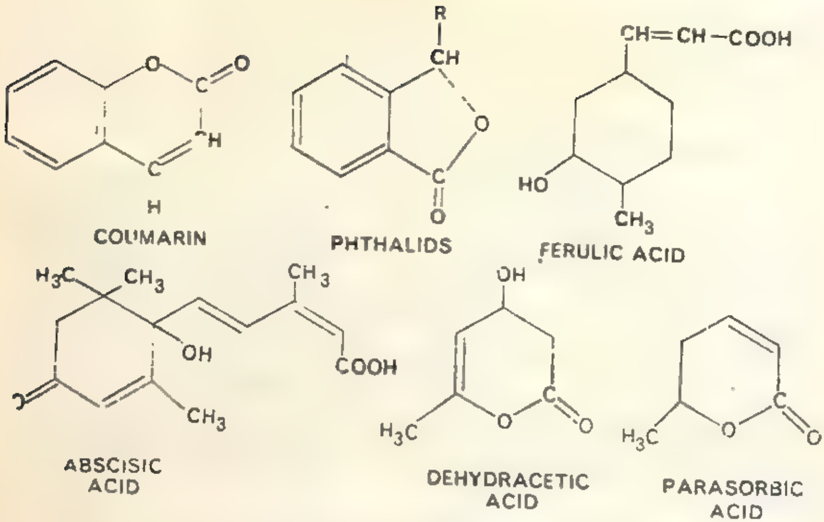


Fig. 97. Molecular structures of some of the common germination inhibitors.

(7) Chilling (or Low Temperature) Requirement

In certain plants such as apple, rose, peach etc., the seeds remain dormant after harvest in the autumn because they have a low temperature or chilling requirement for germination. In nature this requirement is fulfilled by the winter temperatures. In such case the seeds remain dormant throughout the winter season and germinate only in the following spring.

(8) Light Sensitive seeds

In many species the germination of the seeds is affected by light resulting in seed dormancy. Such light sensitive seeds are called as **Photoblastic.** The seeds of certain plants *e.g.*, lettuce (*Lactuca sativa*), Shepherd's purse (*Capsella bursa pastoris*), pepper-grass (*Lepidium virginicum*), tobacco (*Nicotiana tabaccum*), tomato (*Lycopersicum esculentum*) etc., are **positively photoblastic** and germinate only after they have been exposed to light. On the other hand, the seeds of certain plants *e.g. Helleborus niger, Nigella damascena, Silene armeria* etc., are **negatively photoblastic** and their germination is inhibited by light.

The light sensitivity of many photoblastic seeds declines with age if they are kept in dark under dry storage conditions.

SECONDARY DORMANCY OF SEEDS

Sometimes, the seeds which are capable of germinating immediately after harvest become dormant if kept in environment in which at least one of the factors essential for germination is

unfavourable. This induced dormancy is called as **secondary dormancy of seeds.**

For instance, if the seeds of *Brassica alba* are exposed to high concentration of CO_2, they become dormant and will not germinate for a long time even after the removal of CO_2 from the environment which is otherwise favourable for germination.

However, the secondary dormancy of the seeds can be overcome by low temperature or other treatments.

ARTIFICIAL METHODS OF BREAKING THE DORMANCY OF SEEDS

Various methods are employed for breaking the dormancy of seeds depending upon its cause and the particular plant species.

(1) Scarification

The process of rupturing or weakening the seed coats by mechanical or other means is called as **scarification** and is employed in those cases where the dormancy of seeds results due to their resistant or impermeable seed coats. The scarification can be done either **mechanically** by thrashing the seeds by machines or by hands, or **chemically** by treating them with strong mineral acids. Care should be taken during scarification so that the embroys are not damaged.

(2) Pressures

In certain plants *e.g.*, sweet clover (*Melilotus alba*) and alfalfa (*Medicago sativa*) the germination of seeds can be improved by 50-200 percent if the seeds are subjected to hydraulic pressures of 2000 atm. at 18°C for about 5-20 minutes. This effect of pressure on germination results due to changes in the permeability of the testas to water.

(3) Low Temperatures

In many species seed dormancy resulting from chilling requirements can be overcome if the seeds are treated in moist medium at low temperatures (5-10°C) for sufficient period of time. This process is called as **stratification**. Artificial stratification is done by alternating the layers of seeds with layers of wet *Sphagnum* (peat moss), sand or some other suitable material and keeping them at low temperatures.

Low temperatures are also known to overcome the dormancy of certain light sensitive seeds such as lettuce.

(4) Alternating Temperatures

An alternation of low and high temperatures (the difference of the two being not more than 10° or 20°C (greatly improves the germination of seeds in certain plants such as *Poa pratensis.*

Alternating temperatures of 15°C and 25°C daily can also overcome the dormancy of certain positively photoblastic seeds such as *Rumex crispus*.

(5) Light

- The dormancy of positively photoblastic seeds can be broken by exposing them to red light (most effective near 660 mμ) or white light.

- Within limits the germination response depends upon the quantity of light received.

- The effect of red light is reversed by far-red light (maximum inhibition is near 735 mμ).

- Inhibitory effect of the far-red light declines if the far-red irradiation is delayed.

- The inhibitory effect of far-red irradiations can in turn be reversed by subsequent red irradiations.

- This promotion of germination by red-light and inhibition by far-red light probably involves the operation of a proteinaceous pigment called as **phytochrome**. This pigment occurs in two forms, one red absorbing and the other far-red absorbing. Both these forms are photochemically interconvertible. The red absorbing form (P_R) after absorbing the red light is converted into far-red form (P_{FR}). The latter absorbs the far-red light and is converted back into red absorbing form of the pigment.

$$P_R \underset{735\ m\mu}{\overset{660\ m\mu}{\rightleftharpoons}} P_{FR}$$

It is considered that in positively photoblastic seeds *e.g.*, pepper grass, lettuce etc., the far red absorbing form of the pigment is stimulatory to seed germination while red-absorbing form is inhibitory to seed germination.

(6) Germination Stimulating Compounds

The effects of kinetin and gibberellins in inducing the germination of certain positively photoblastic seeds such as tobacco, lettuce etc., even in dark is well known. Besides them, a number of other chemical compounds are also known to possess germination stimulating capacity in certain seeds. Most common of these are KNO_3, thiourea and ethylene.

ADVANTAGES OF DORMANCY OF SEEDS

(i) In temperate zones the dormancy of seeds helps the plants to tide over the severe colds which may be injurious for their vegetative and reproductive growth.

(ii) In tropical regions the dormancy of seeds resulting from their impermeable seed coats ensures good chances of survival.

(iii) Dormancy of seeds in many cereals is of utmost importance to mankind. If these seeds would germinate immediately after harvest in the field, they will become useless to man for consumption as food.

16

Plant Movements

PLANT MOVEMENTS

Movements in plants (Fig. 98) are of 3 types :—

(A) Movements of Locomotion
(B) Movements of Curvature
(C) Hygroscopic Movements

The first two types of movements are called as **vital movements** because they are exhibited only by the living cells or organisms.

(A) MOVEMENTS OF LOCOMOTION

Those movements in which whole of the plant body or the cell or cytoplasm moves from one place to another are called as **movements of locomotion**. These movements may occur either **spontaneously** or in response of a certain **external stimulus** and are called as **autonomic** and **paratonic** (or **induced**) movements respectively. Paratonic movements of locomotion are also known as **tactic movements**.

(a) Autonomic Movements of Locomotion

(1) **Ciliary movements**. Such type of movements take place due to the presence of cilia or flagella *e.g.*, *Chlamydomonas*, *Volvox*, flagellated bacteria, flagellated or ciliated reproductive cells etc.

(2) **Amoeboid movements.** Such movements are exhibited by **Myxomycetes** where the naked **plasmodium** moves by producing **pseudopodia** like an *Amoeba*.

(3) **Cyclosis**. In living cells of many plants the cytoplasm including various cell-organelles moves around the vacuoles. This movement of the cytoplasm is called as **protoplasmic streaming** or **cyclosis**. It is of two types—**rotation** and **circulation.**

In rotation, which is exhibited by plants like *Chara, Hydrilla Vallisneria, Elodea* etc., the cytoplasm moves either clockwise or anti-clockwise around a larger central vacoule. While in circulation, which is exhibited by the cells of **staminal hairs** of plants like *Tradeschantia*, the cytoplasm moves in both clockwise and anti-clockwise directions around many smaller vacuoles.

(b) Paratonic or Induced Movements of Locomotion or the Tactic Movements or Taxes.

(1) Phototactic movements or phototaxis. These movements occur in response of an external stimulus, the **light** and are exhibited by zoospores and gametes of certain algae *e.g., Clamydomonas, Volvox. Ulothrix, Cladophora* etc. They show a positive phototactic movement under diffused light and a negative phototactic movement under intense light.

(2) Chemotactic movements or chemotaxis. These movements occur in response of an external **chemical stimulus**. Such movements are exhibited most commonly by the antherozoids in bryophytes and pteridophytes where the archegonia secrete some chemical substances having a peculiar odour towards which the antherozoids are attracted chemotactically.

(3) Thermotactic movements or thermotaxis. Such movements result due to an external **heat stimulus**. For instance, if a large vessel containing some *Chlamydomonas* in cold water is warmed on one side, the *Chlamydomonas* cells will move and collect towards the warmer side (positive thermotaxis). However, a negative thermotaxis will occur if the temperature becomes too high.

(B) MOVEMENTS OF CURVATURE

In higher plants which are fixed, the movements are restricted only to the bending or curvature of some of their parts. Such movements are called as **curvature movements** and may be either **autonomic** *i.e.*, spontaneous or **paratonic** *i.e.*, induced. The curvature movements may be of two types—**variation movements** and **growth movements**. In variation movements the curvature or the bending of the plant part is **temporary** while in growth movements it is of **permanent** nature.

(a) Autonomic Movements of Curvature

(1) Autonomic movements of variation. Telegraph plant (*Desmodium gyrans*) is an excellent example of such movements. In this plant the compound leaf consists of a larger terminal and two smaller lateral leaflets (Fig. 98). During day time, the two

lateral leaflets exhibit peculiar and interesting movements. Sometime they move upward at an angle of 90° and come to lie parallel to the rachis. Again, they may move downward at 180° so that they are parallel to the rachis. They may again move upward at 90° to come in their original position. All these movements occur with jerks after intervals, each movement being completed in about 2 minutes.

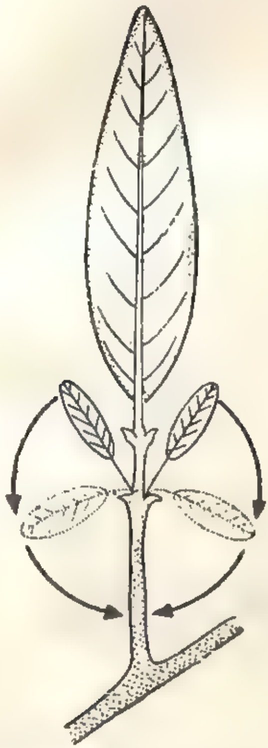


Fig. 99.. Autonomic variation movements in the leaf of Telegraph plant.

(2) Autonomic movements of growth

(i) **Hyponastic and epinastic movements.** These movements occur in bifacial organs like young leaves, flower sepals, petals etc., and result due to the differential growth on the two sides of such organs. For instance, if there is more growth on the lower side of sepals and petals the flower will close. Such movements are called as **hyponastic movements**. On the other hand, if there is more growth on their upper side the flower will open. Such movements are called as **epinastic movements**. Examples of these nastic movements may be found in ferns where the leaves (fronds) become circinately coiled in young condition (hyponasty) and erect in older condition (epinasty) or in the opening and closing of flowers in many plants such as *Crocus*.

(ii) **Nutational movements.** Sometimes the growth of the stem apices occur in a zig-zag manner. It is because the two sides of the stem apex alternatively grow more. Such growth movements are called as **nutational movements** and are common in those stem apices which are not strictly rounded but slightly flattened.

(iii) **Circumnutational movements.** In strictly rounded apices the growth occurs in a rotational way. It is because the region of maximum growth gradually passes round the growing apex. Such movements are called as **circumnutational movements.**

(b) Paratonic Movements of Curvature.

(1) **Paratonic movements of growth or tropical movements or tropisms**. When growth movements occur in response of an external stimulus which is **unidirectional**, they are called as **tropical movements**. And the phenomenon of such a movement is called as **tropism**. Depending upon the nature of the unidirectional external stimulus the tropical movements are of many types :—

(i) **Geotropic movements or geotropism**. The tropical movements which take place in response of the **gravity stimulus** are called as **geotropic movements** and this phenomenon as **geotropism**. The primary roots grow down into the soil and are **positively geotropic**. The secondary roots growing at right angles to the force of gravity are called as **diageotropic**. On the other hand, the primary stems are **negatively geotropic**.

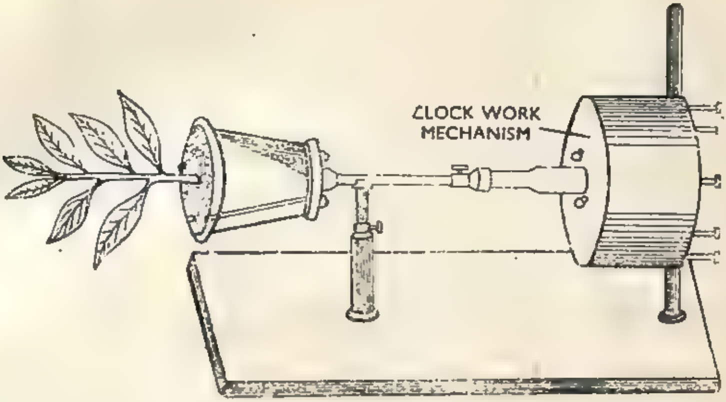
Geotropism in primary roots and stems can easily be demonstrated by sowing certain maize seeds in the soil so that their radicles lie in different directions. After a few days it will be noticed

Fig. 100 Geotropism in maize seedlings.

that irrespective of their position, the radicles in all the seeds always go down while the coleoptiles always grow in upward direction (Fig. 100).

That the geotropic curvature results due to unilateral gravity stimulus can be demonstrated by using a **clinostat** (Fig. 101). If a young potted plant is fixed on a clinostat in horizontal position and rotated, neither the root will bend down nor the stem will curve upward. It is because in such case, the effect of gravity will be uniform all round the stem and root. If however, the plant lies in horizontal position and is not rotated, the stem and the root will receive gravity stimulus only on their lower sides or the effect of gravity will be unilateral. This will result in a positive geotropic curvature in root and negative geotropic curvature in stem.

In case of roots, the gravity stimulus is perceived **only by the root tip**. However, the geotropic curvature takes place a little behind the root tip, in the **region of cell elongation**. The effect of the unilateral stimulus of gravity causes **unequal distribution** of growth hormone **auxin** in the root tip *i.e.*, more auxin concentrates on the lower side than on the upper side. This in turn results in more growth on the upper side and less growth on lower side, and ultimately a positive geotropic curvature is observed (Fig. 102.)



Ffg. 101. Clinostat.

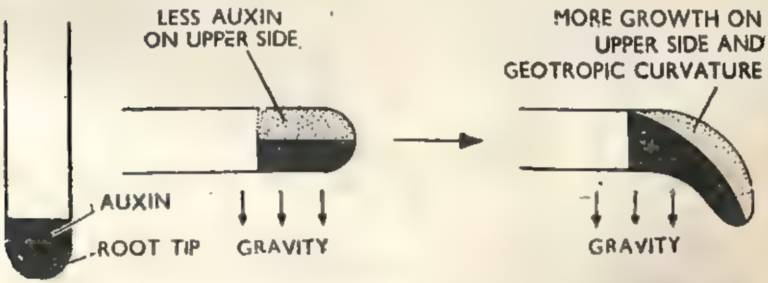


Fig. 102 Interaction of gravity and auxin in causing geotropic curvature in root tip.

However, in case of stem the higher concentration of auxin on the lower side promotes more growth on that side so that a negative geotropic curvature is observed.

(ii) **Phototropic movements or phototropism.** The tropical movements which occur in response of an external unilateral

light stimulus are called as **phototropic movements**. These movements are commonly found in young stem tips which curve towards the unilateral light stimulus and thus, are called as **positively phototropic**. This can be observed very easily by placing a potted plant in a room near an open window. After a few hours, the stem will be seen bending towards the window, the latter being the unilateral source of light (Fig. 103). The roots in some plants also exhibit phototropic movements but they are **negatively phototropic**.

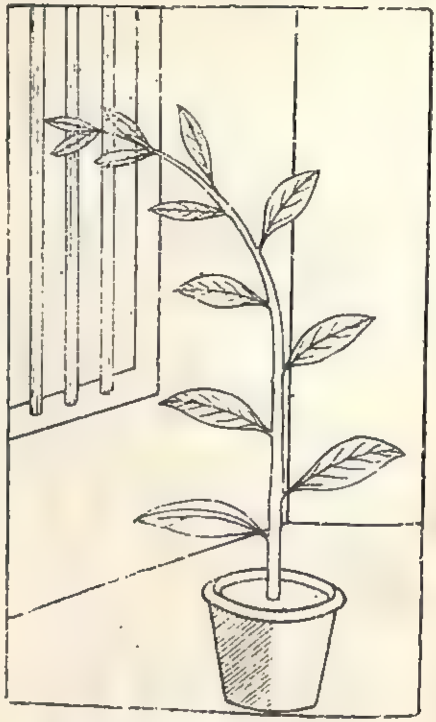


Fig. 103. Stem is positively phototropic.

When the stem tip receives uniform light all around, the concentration of the growth hormone **auxin** also remains uniform in the tip. But when the tip receives unilateral light, the conc. of auxin becomes more in the shaded side than in the lighted side. Consequently, the higher conc. of auxin in the shaded side causes that side to grow more resulting ultimately in a positive phototropic curvature (Fig. **104**).

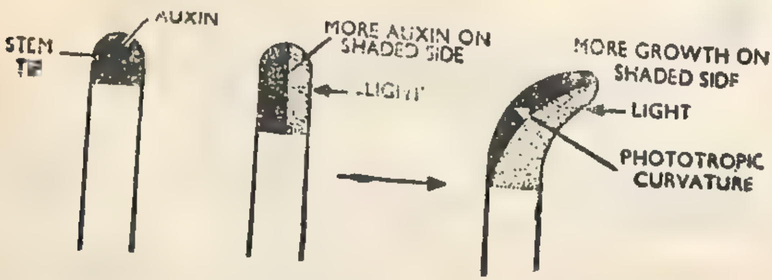


Fig. 104 Interaction of light and auxin in causing phototropic curvature in stem tip.

If, however, a small young potted plant receiving unilateral light is fixed on a **clinostat** in a vertical position and rotated, there will be no phototropic curvature in the stem. It is because in this

case the stem tip will be receiving unilateral light all around its tip and there will be no unequal distribution of the auxin.

(iii) Thigmotropic or haptotropic movements. These movements take place in response of a touch or **contact stimulus** and are very common in plants which climb by **tendrils** (Fig. 105).

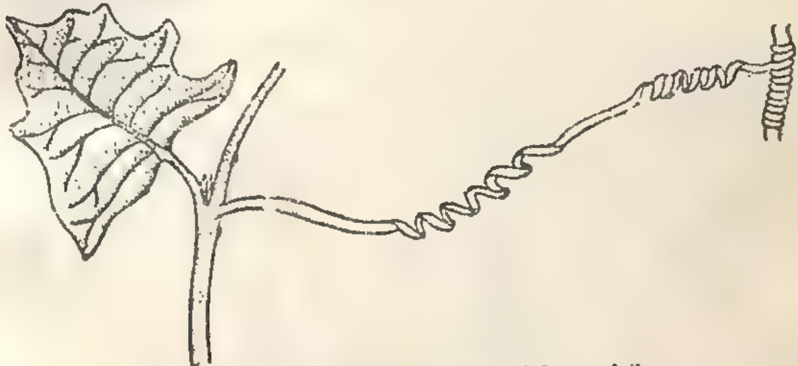


Fig. 105. Thigmotropic curvature of the tendril.

In such plants *e.g.*, *Passiflora*, the tip of the tendril in the beginning moves freely in the air. But as soon as it comes in contact with a solid object which may provide it support (*i.e.*, it gets the contact stimulus), it twines round the object so that the plant may climb upward. The twining of the tendril around the support is due to less growth on that side of the tendril which is in contact with the support than the more growth on the free opposite side.

(iv) Hydrotropic movements or hydrotropism. The tropical movements occurring in response of water stimulus are called as **hydrotropic movements**. These are commonly found in young roots and can be demonstrated by the following simple experiment :

Fig. 106 Experiment to show hydrotropism.

Some seeds soaked in water the previous night are kept on a wire gauze covered with saw dust. The wire gauze is then kept slanting in humid condition. After a few days, the radicles will be seen bending towards the moist saw dust (Fig. 106).

(v) Chemotropism. Chemotropic movements occur in response of some

chemical stimulus and are best exhibited by fungal hyphae and pollen tubes.

(vi) **Thermotropism and Aerotropism**. These tropical movements are not very important. When they occur in response of temperature stimulus, they are called as **thermotropic movements.** In case the stimulus is air, they are called as **aerotropic movements.**

(2) **Paratonic movements of variation or nastic movements.** When growth movements occur in response of an external stimulus which is not unidirectional but **diffused,** they are called as **nastic movements** These movements occur only in bifacial structures like leaves, sepals, petals etc., and may be of many types :

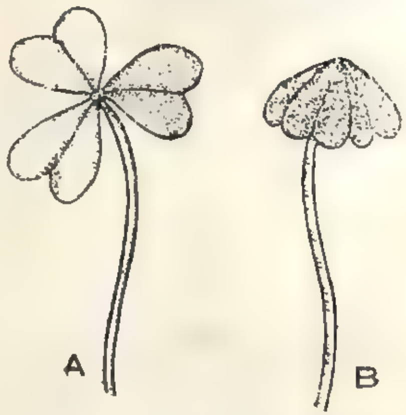


Fig. 107 Photonastic movements in *Oxalis* leaf. A. during day; B. During night.

(i) **Nyctinastic movements (or sleep movements).** In many plants the leaves and flowers aquire a particular but different position during day and at night. Such movements are called as **nyctinastic movements** or **sleep movements.** If these movements result in response of the presence or absence of light, they are called as **photonastic movements** *e.g., Oxalis* sp. (Fig. 107) where the flowers and leaves open in the morning and close at night. In other plants such as *Crocus* and *Tulip* the fl wers open at higher temperatures and close at low temperatures. Such movements which occur in response of temperature stimulus are called as **thermonastic movements.**

(ii) **Seismonastic movements.** These movements are best exhibited by **sensitive plant** (*Mimosa pudica*) and occur in response of a **touch or shock stimulus.**

In this plant the leaves are bipinnately compound with a swollen **pulvinus** at the base of each leaf and similar but smaller **pulvinules** at the bases of each leaflet or pinna. If a terminal pinnule of a leaflet is touched or given a shock treatment, the stimulus passes downward to the pulvinule and all the pinnules of that leaflet get successively closed in pairs. Now the stimulus passes to the other pinnae or leaflets so that their pinnules also close down and finally reaches the pulvinus resulting in drooping of whole of the leaf (Fig. 108 A, B). Whole of this process is completed just in few seconds.

The lower half of the pulvinus consists of thin walled parenchymatous cells with larger intercellular spaces while the upper half consists of slightly thick walled parenchymatous cells with very small and fewer intercellular spaces. In normal condition the cells of both the halves remain fully turgid (Fig. 108 C) but when the stimulus reaches the pulvinus the **osmotic pressure** of the cells of

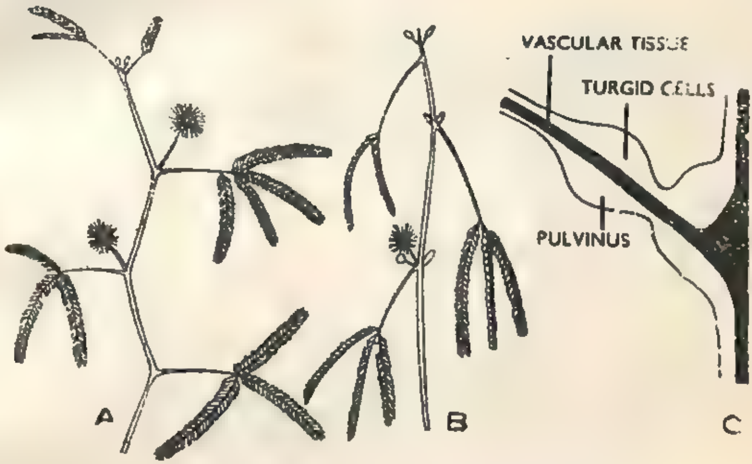


Fig. 108. Seismonastic movements in *Mimosa pudica*.
A. Unstimulated leaf; B. Stimulated leaf;
C. Diagrammatic section of the pulvinus.

the lower half becomes lower and they release water into the intercellular spaces to become **flaccid** or **less turgid**. On the other hand, the cells of the upper half maintain their turgidity and may even absorb some water to become **more turgid**. The pressure of the upper turgid half on the lower flaccid half results in drooping down of the leaf.

After the lapse of some time, the leaf recovers from the shock or touch stimulus and again comes in its normal erect position.

It is believed that the stimulus travels down to the pulvinus in the form of a **hormone** through the xylem where it causes the changes in osmotic pressure and turgidity of the parenchymatous cells of the lower half of pulvinus resulting in drooping down of the leaf. After sometime, the osmotic pressure of these cells increases so that water returns back into them from the intercellular spaces, the cells again become turgid and the leaf comes to its normal erect position.

(iii) Thigmonastic or haptonastic movements. These movements are found in the leaves of *Drosera* (Sundew) and *Dionaea* (Venus Fly Trap) and result in response of the touch stimulus of the insects. In *Drosera*, as soon as an insect sits on the leaf, the

tentacles curve inward to trap the insect. Similarly in *Dionaea*, the two halves of the leaf curve upward along the mid-rib. These parts of the leaves come to their normal position after the insect has been digested.

(C) HYGROSCOPIC MOVEMENTS

These movements are found only in dead parts of the plants which are hygroscopic in nature and result either due to loss or gain of water by them from the atmosphere. Hygroscopic movements can best be observed in the elaters in bryophytes, peristome teeth in moss capsules, elaters of *Equisetum* spores etc.

ECOLOGY

I

ECOLOGY

The things of the world are classified into two major groups, namely, the living or biotic component and the non-living or abiotic component. The biotic component includes all types of living organisms, both plants and animals and the abiotic component includes the non-living materials (soil, water, air etc.) and the forces of nature (light, gravity and molecular energy). The living organisms exist in an environmental setting of which they are a part. Every aspect of life is influenced by the environment and the activities of organisms affect their environment. An aspect of biology which deals with the inter-relationship between biotic and abiotic components as well as the relationships among the individuals of the biotic component is called ecology. Organisms form interacting systems or communities, these communities are coupled to their environments by transfer of matter and energy and the communities and environment are interrelated. A functional system formed by communities and their environment is called *ecosystem*. The ecology is a science of ecosystems or totality of reciprocal interactions between living organisms and their physical surroundings. (Clark, M.E., 1973).

The word 'ecology', first proposed by a zoologist named **Reiter** in 1885, is derived from Greek words, *oikos* meaning the dwelling place or home and *logos* meaning the discourse or study ; thus, the word ecology literally means the study of living organisms, both plants and animals, in their natural habitats or homes. **Odum** has defined ecology as *the study of the structure and the function of nature.* This branch of science seeks to determine the effects of environmental factors on the growth, distribution and migration of the

organisms and also deals with some other aspects of relationship between organisms and these factors.

Ecology, like biology, has been subdivided into plant ecology and animal ecology. Plant ecology deals with the relationship between plants and their environments and animal ecology is concerned with the study of relationship between animals and their environments. Ethology is the name now generally used by biologists to denote the scientific study of animal behaviour with special reference to the behaviour of animal in its normal environment. In recent years there has grown an idea that in biological organisation the plants and animals are closely interdependent and they react with one another in many ways and at a particular place plants and animals share the same set of conditions and same environment. Therefore, these two sub-divisions, plant ecology and animal ecology should be unified. In view of this reasonable fact, the authors of modern ecology have accounted for the study of both plants and animals in the environment.

Ecology and its Divisions

Ecology may be divided into **autecology** and **synecology**.

Autecology. Autecology is concerned with the study of individual animal or plant species or its population throughout its life history in relation to the habitat in which it grows, or in other words, it is a study of inter-relationship between individual species or its population and its environment.

Synecology. The other area of ecology which deals with systems of many species—whole communities or major fractions of communities and ecosystems is termed *Synecology* in English speaking countries, *biocenology* or biosociology by many Europeans. (Whittaker, R. H. 1970).

It is concerned with the structure, nature, development, and causes of distribution of communities. To understand the ecology of plant communities, the ecological life cycles (autecology) of at least most important plant species of the communities must first be studied. Thus, autecology forms a basis for the study of synecology.

The study of plant community structure is called phytosociology or plant sociology. The study of plant ecology merges with plant geography or phytogeography. This is a science which deals with the distribution of plants on or near the surface of earth and water and it also deals with the migration of species. Actually speaking there is no sharp line of distinction between plant ecology

and plant geography. **W. B. Turrill** comments *that plant ecology is intensive while plant geography is extensive in outlook, but both are concerned with plants and in attempting to correlate observed structure and behaviour of plants with causes, both refer to the same sum total of environmental factor though the emphasis varies.*

Different Fields of Ecology

Different branches which are made to account for the various specific and detailed aspect of ecology are as follows :

1. **Habitat Ecology**. It deals with habitat as a central theme and plants and animals as only inhabitants. It includes forest ecology, grassland ecology, fresh water ecology, marine ecology, desert ecology, etc.

2. **Paleoecology**. It is concerned with the organisms and geological environments of the past.

3. **Cytecology**. It deals with the cytological details of the species of populations in relation to different environmental conditions.

4. **Ecosystem ecology**. It deals with the structure and working of ecological systems in relation to space and time and also with the analysis of components of ecosystem. In this, special emphasis is laid on the reciprocal relationship between living and non-living systems.

5. **Conservation ecology or Resource ecology**. It is concerned with the proper management of plant, animal. soil, water and mineral resources for human welfare.

6. **Ecological energetics and Production ecology**. These modern branches of ecology are still in developing stage. These deal with the mechanisms and quantity of energy conversion and flow of energy through organisms. Energy production processes, rate of increase in organic weights of organisms in relation to space and time are also discussed in this branch of ecology.

Plant Ecology and other branches of Science

Ecology is a synthetic branch of biological science which draws source materials from many other sciences. It is fundamentally related to morphology, taxonomy, physiology, biochemistry, cytology, genetics etc. Various other sciences, such as, physics, mathematics, statistics are also being increasingly used in the study of ecological problems. Application of radioactive isotopes, use of many modern and advanced instruments like spectrometer, infrared gas analyser,

flame photometer, computers in the analysis of data, calorimeters, phytotrons for culturing the plants in environment controlled chambers and many other equipments are widely used in ecological researches. Besides botany, zoology, chemistry and physics, the knowledge of climatology, geography, pedology and geology is also essential in the study of complicated problems of plant ecology.

Application of plant ecology

The study of plants in their environment has yielded a large body of knowledge which provides aids to the science of conservation of natural resources. The knowledge of ecology is of great help in controlling soil erosion, reforestation, restoration of wild animals as well as grassland vegetation, and flood control. Plant ecology is directly related to silvics, and silviculture and other branches of forest biology. In *British Commonwealth Forestry Terminology* (1953), **Silvics** has been defined as the study of general characteristics and life history of forest trees and crops with particular reference to environmental factors, as the basis for practice of silviculture while the **Silviculture** has been defined as the art and science of culturing forest trees and crops.

Every farmer or gardener is ecologist, since by such practices as cultivation, irrigation, artificial pollination and spraying, he affects the plant behaviour.

Knowledge of ecology is being applied in agriculture, food production and horticulture. The soil conservation practices are in use these days in agronomy. The modern ecology revolves round the biological production processes and ecological energetics. The International Biological Programme (IBP) was launched since July 1, 1967 to study the biological basis of organic productivity and conservation of natural resources in relation to human welfare. Launching of this programme has given impetus to the ecologists all over the world and over 70 nations including India have participated in the IBP studies at either national or international level. The future of ecology and indeed of Biology is likely to be changed by some international programmes such as 'Man and biosphere' (MAB).

The history of ecology in India is not very different from that of any other country in the world. Indeed, it has been much influenced by western school which provided the leadership. Publications of botanical explorations by Dudgeon (1920)., Saxton (1922), Bor (1942), Osmaston (1926) and Champion (1936) provided enough opportunity for ecological investigation in India. Professor F. R. Bharucha, a student of Braun-Blanquet, established the first school

of ecology at Bombay. This school contributed a great deal of information on the biological spectra of different regions of India and on the phytosociology of grass and forest vegetation. The second school of ecology was developed under the leadership of Professor R. Mishra first in Sagar and later at Varanasi. At present, many secondary schools of ecology are emerging at Ujjain, Ahmedabad, Pilani, Jodhpur, Pondicherry etc., and ecologists in these centres are engaged in different fields of study.

QUESTIONS

1. What is ecology ? How it is related with other branches of biology ?
2. What are different branches of ecology ? Why study of ecology is important for man ?

2

THE ENVIRONMENT

In ecology, the reciprocal relationship between an organism or a group of organisms and its environment is studied. The environment literally means the surrounding. The environment is the aggregate of all those things and set of conditions which directly or indirectly influence not only the life of organisms but also the communities at a particular place. It is comprised of a number of factors, which interact with one another and also influence the responses of the organisms. Any external force, substance or condition affecting the organisms in any way is referred to as environmental factor. Soil, moisture, wind and temperature are, thus, factors and the environment, thus, is the sum total of all such factors. The natural place where organisms of communities of organisms live is called *habitat*. The habitat implies a particular set of environmental factors and is, therefore, generally used in a more concrete sense than the environment.

All the living organisms on earth are confined to the thin outer shell of atmosphere, ocean and earth crust. The life supporting environment of planet earth is called biosphere. The biosphere is composed of three chief media—air, soil and water and on this basis biosphere has been divided into three sub-divisions : *Atmosphere*, *lithosphere* and *hydrosphere* respectively.

In an ecosystem the species and its environment are taken as a complex *Whole*. Environment, as pointed out earlier, in itself is a complex of factors acting, reacting and interacting with the organism complex.

Ecological factors are many and diverse and often intricately

mixed and interdependent. These factors, either singly or in combination influence and determine the presence or absence, vigour or weakness, and relative success or failure of various plant communities in a particular habitat.

Main environmental or ecological factors

The environmental conditions which influence the life and development of plants are grouped into four main classes which are as follows :

(1) Climatic factors (related to aerial environment) ;
(2) Edaphic factors (related to soil conditions) ;
(3) Physiographic (topographic) factors ; and
(4) Biotic factors

As already mentioned, these ecological factors are inter-related and intricately mixed. They work through one another acting and reacting together, as for example, the change in physiographic conditions at a place may bring about a change in local climate that, in turn, may affect the soil and competition impress.

CLIMATIC FACTORS

Climate is one of the important natural factors controlling the plant life. Its study is called climatology. The climate includes the following main factors :

(1) Light
(2) Temperature
(3) Precipitation and atmospheric humidity
(4) Wind

LIGHT

Sun is the ultimate source of all energy that sustains life on this earth. This energy is trapped by green plant when chloroplasts convert radiant energy into chemical energy. Radiant energy is in the form of electro-magnetic waves. The wave lengths of visible light vary from 400 $m\mu$ to 750 $m\mu$. These are involved in photosynthesis. Below this range is ultraviolet and above infrared. Light affects through its quality, intensity and duration on the various processes. Its direct effect is on :—(*a*) Formation of chlorophyll (*b*) Photosynthesis (*c*) Photoxidation (*d*) Photoperiodism and (*e*) Phototropism. Indirectly it affects absorption of water, transpiration, respiration etc. etc.

The quality of light is seldom a factor of ecological inportance because of little variations in natural conditions.

The **intensity** of light is affected by altitude, atmospheric gases, water vapours, dust particles, vegetation, geographical conditions. Intensity of light is measured in lux or meter candle or foot candle abbreviated as L. M. C. or F. C. L. or M. C. denotes the amount of light which is received at a distance of one meter from standard candle while in F. C. the distance is one foot. Lux which is equivalent to App. 0·0929 F.C. is recognised as an international unit. The maximum intensity of light to which a plant may be exposed at an altitude of 3000 meters may be 20% more than that of at the sea level. Of the atmospheric gases nitrogen and oxygen chiefly possess property of absorption and dispersion of shorter wave lengths. Water vapours reduce light intensity. On a cloudy day the reduction may be 96%. The intensity goes on decreasing as light rays penetrate into deeper layers of water. At 50 meter deep practically no photosynthesis is possible. But photosynthesis may continue under 0·4 meter of snow cover. In industrial areas smoke may reduce the intensity to 10% of normal. The presence of dust particles on the plant surfaces also reduces light. The intensity is also effected by the foliage of trees. Under the thick canopy of forest trees no growth of plants may be possible underneath the trees. The direction and slope also affect intensity. Direct light may not be there at all or feeble on one side of the slope. Light intensity shows diurnal variations. It is at its maximum during midday when sun is overhead and declines gradually toward mornings and evenings.

Importance of light to plants

Light affects many physiological activities of the plants. Light affects the following aspects of plant life :

(1) **Photosynthesis.** Out of the total solar energy reaching to the earth, only about 2% is used in photosynthesis and about 10% is used in other physiological activities. It has been estimated that a corn plant utilises only 0·13 per cent of light energy. All wave lengths of light are not utilised by a plant. Green light is completely reflected by green parts of the plants making them look green. Red and blue green are the two maxima of absorption of light. The green plants, the producers of ecosystem, synthesize their food (carbohydrates) from water and CO_2 in presence of sun light. The solar radiations provide energy for this process. In this process radiant

energy of the sun available to the plants is converted into the chemical energy by chlorophylls. The chemical energy stored in food is utilised in various other biochemical activities in the plants. The rate of photosynthesis is greater in intermittent light than in the continuous light. The relationship of light intensity with photosynthesis in terrestrial as well as in aquatic plants follows the general pattern of a linear increase upto an optimum or saturation intensity followed by a decrease at high intensities (Rabinowith, 1951 ; Thomas, 1955).

Light plays important role in the development of plastids and pigments. It has marked effect on the number and position of chloroplasts. The upper part of leaf which recieves full sunshine has large number of chloroplasts which are arranged in line with the direction of light. At high intensity, the photo-oxidation of enzymes reduces not only the rate of carbohydrate synthesis but also that of protein synthesis. The protein synthesis is especially reduced by high intensity of light. High intensity of light, however, influences the formation of anthocyanin pigment. It is for this reason, alpine plants have beautifully coloured flowers.

(2) **Respiration**. There is no direct effect of light on the respiratory activity in the plant body. Indirect effect is much important because in presence of light the respiratory substrates are synthesized. Under certain conditions, such as, in shade and under water, the light becomes a limiting factor and the photosynthesis is not sufficient for effective growth. Under such conditions, the rate of photosynthesis is just sufficient to meet the need of respiration. This is called *compensation point*. At this point, the dry weight of plant does not increase. The compensation point differs in different species and in different individuals of the same species at different ages. In many plants the respiratory rate increases with the increase in the light intensity. Ranjan and Saxena have studied the effect of light intensities on respiration rate in many plants and have shown that respiratory rate could increase in *Canna*, *Nerium*, *Bougainvillea* with the increase in light intensity. However, in some other plants respiration rates decreased slightly in intense light. The rise and fall of respiration rate may be due to the effect of light on the permeability of plasma membrane, change in the viscosity of the protoplasm and photo-oxidation of enzymes. The permeability and viscosity increase with the increase in light intensity up to certain optimum. Light, however, has got very little effect in respiratory process of lower plants and thallophytes.

(3) **Opening and closing of stomata and in transpiration**. Mostly the stomata remain opened in the light and closed in the dark. Light brings about phosphorylation and conversion of starch into soluble sugars in the guard cells and thereby increases their osmotic pressure which, in turn, causes inflow of water in the guard cells. The increase in the turgidity of guard cells causes widening of gap between two guard cells. The opening of stomata increases the gaseous exchange and also increases the rate of transpiration during day period. Increase in the light intensity above the optimum shows detrimental effects because the increased transpiration in the intense light is injurious to plants.

(4) **Growth and flowering of plants**. Light shows manifold effects on the growth of the plants. Growth of plants depends especially on the intensity, quality, duration and direction of light. High intensity of light inhibits the production of auxins or growth hormones and consequently it influences the shapes and sizes of plants. Plants growing in darkness or insufficient light produce maximum amount of growth hormones as a result of which they are elongated with slender pale yellow stem and small leaves. The plant growth is slow in the light of high intensity. Red light favours the growth. Lights of shorter wavelength, except violet, are deterimental to plant growth.

Duration of light is also very important. Actual duration or length of the day (photoperiod) has been shown to be important factor in the growth and flowering of wide variety of plants. The controlling effect of the photoperiod, known as photoperiodicity, is currently an active field of physiological ecology. According to their response to length of photoperiods, the plants have been classified into three well defined groups :

(i) **Long day plants**. Plants which bloom when the light duration is more than 12 hours per day, as for example, radish, potato, spinach, etc.

(ii) **Short day plants**. Plants which bloom when the light duration is less than 12 hours per day, as for example, cereals, tobacco, cosmos, dahelia, etc.

(iii) **Day neutral plants**. Plants which show little response to length of daylight, as for example, tomato plant.

Recently it has been shown that photo-periodic stimulus for flowering is also controlled by thermal points. Azzi (1957) has shown for the first time that initiation of flowering in a plant occurs at

certain constant which is specific for a particular species. This constant is called Azzi's constant which is expressed as follows :

Azzi's constant = Total duration of light in hours
+ total mean temperature in °C.

Chinoy (1960) has confirmed this constant and called it **Photo-thermal quantum** requirement of a species. Thus, an increase in temperature will decrease the duration of light required for flowering. This information can be applied to advantage in autecological studies of certain crop plants.

Plants which receive direct sunlight are called *heliophytes* and those growing in the shades are called *sciophytes*.

Heliophytes exhibit the following features :

(*i*) Stem with short internodes and long lateral organs ;
(*ii*) Roots numerous and profusely branched ;
(*iii*) Thick cuticle ;
(*iv*) Well developed palisade and weakly developed spongy tissue in the leaf ;
(*v*) Well developed xylem with thick rays ;
(*vi*) Small intercellular spaces in the tissues ;
(*vii*) High respiration rate and much rapid transpiration ;
(*viii*) Vigorous flowering and fruiting ;
(*ix*) Early appearance of flowers ;
(*x*) Low chlorophyll content ; and
(*xi*) Proper development of mechanical tissues.

In the absence of light, the growth is very poor and plants show etiolation. The stem becomes tender, narrow, and long and the leaves become pale green, soft and small. Thus, light is essential for the normal and healthy growth of plants.

(5) **Movement**. Light affects the movement in some plants. The stems, roots and leaves show different response to light. The effect of sunlight on the plant movement is called heliotropic effect. The stems elongate toward the source of light (positively phototropic) and the roots are negatively phototropic. The leaves grow transversely to the path of light. In order to receive maximum sunlight, the leaves are oriented on the stem in such a way that they do not overlap each other.

(6) **Germination of Seeds**. The seeds when moist are very sensitive to light. In some cases, the germination of seeds is retarded

in light. The quantity of light needed for the stimulation of embryo varies in different seeds.

Light is an important factor in the distribution of plants. Some plants grow in full sunlight, while others prefer to grow in shade. Bormann (1956) describes an interesting situation in certain species of pine in which young seedlings are shade adapted while older seedling and young trees do not grow well in shades.

TEMPERATURE

The most influential factors in the climate are temperature and moisture. The temperature affects the vegetation either directly or indirectly. Directly it appears in two way :

(*i*) It affects the physiological processes of plants and consequently their growth and size ; and

(*ii*) It determines which species can survive in a particular region. The different species of plants show a wide variation as regards their tolerance to temperature range and fluctuation.

On our planet, organisms can carry on their life activities over a relatively narrow temperature range extending from 0°C to 50°C and every plant has a specific range of temperature requirement. This range differs from species to species. Plants do not thrive in places with higher or lower temperatures than their ranges.

Generally, at 40°C the protoplasm undergoes such changes as minimal to plant life and it dies at temperatures above 90°C. However, some plants carry on their life processes at high temperatures but at 70°C temperature plants rarely survive. At temperatures below freezing point plants generally die because of rapid crystallisation of protoplasmic water which results in mechanical injury. Air dried yeast can endure temperature as high as 114°C. Bacteria can endure temperature between 120°C and 130°C. A few fungi can withstand temperature upto 89°C. Air temperature above 32°C is most favourable for tropical plants. Existence of vegetation has been recorded between 26°C (some conifers) to 66°C (Desert plants). The temperature range can be said minimum, optimum (most suitable temperature for life and growth) and maximum (beyond which no survival is possible)

The general inability of protoplasm to endure high temperature can be ascribed in large part to the sensitivity of its enzymes to heat. Catalytic proteins in nearly all cases are irreversibly inactivated by exposure to high temperatures (usually greater than 50°C) for any

length of time. They are, however, able to withstand lower temperatures even below the freezing point of water. The ability of the cell to endure sub-freezing temperatures seems to depend principally upon the avoidance of ice formation. The appearance of ice crystals in cells is almost always associated with the death of these cells, due in part to mechanical damage inflicted on the subcellular structure by the ice crystals themselves. Death may be also due to removal of water from the protoplasm by ice formation in the intercellular spaces, thus dehydrating the protoplasm.

According to the heat requirement of plants, Raùnkiaer divided the gross vegetation into the following types :

(a) **Megatherms**. Plants of warm habitat which require high degree of heat throughout the year. They are found in areas with tropical climates e.g. plants of deserts

(b) **Mesotherms**. Plants of habitat which is neither very hot nor very cold. These plants cannot stand extremely high or low temperatures and they are found in tropical and subtropical habitats.

(c) **Microtherms**. These are the plants of cold or temperate habitat and require low temperatures for their growth. Such plants cannot tolerate high temperature. They may also be found in tropical and subtropical areas at high elevations where temperature conditions are less extreme.

(d) **Hekistotherms**. These are the plants of cold and alpine regions. They do not thrive well in heat and can stand long very severe winter.

Many plants are very sensitive to temperature. The sudden fall in temperature is injurious because plant tissues are badly affected with it. Forests suffer from night frost on the east side where the sun rays strike very early in the days. As an adaptation against frost, the starch of plants changes to fats or oils in the autumn. The fatty oils depress the freezing point and thus increase the power of resistance in plants against frost. The leaves of plants in the coldest lands store fats. Pentosans, mucilage and pectic substances which have high water retaining power are abundant in many plants. They decrease the danger of plants from desiccation and consequent death. Dried seeds and spores are not affected with freezing because there remains no liquid in them that can freeze. Due to removal of water from seeds, the cold resistance of seeds of certain plants increases up to the extent that their exposure for 3 weeks to $-190°C$, does not diminish their germinability.

The temperature stimulates the growth of seedlings. The optimum temperature for seed germination ranges between 20°C and 27°C.

The absorption rate is retarded at low temperature. Photosynthesis operates over a wide range of temperature. Most of the algae require lower temperature range for photosynthesis than the higher plants. The photosynthesis continues even at 80°C in some desert plants.

The rate of respiration increases with the rise of temperature upto a certain level, but beyond the optimum limit the respiration rate shows marked decrease. The rate of respiratian becomes doubled at the increase of 10°C above the optimum temperature provided other factors are favourable (*Vant Hoff's law*). High temperature generally favours the growth of plants, but for some crop plants low temperatue is beneficial. If the temperature ranges of winter varieties are lowererd upto 0°C to 5°C, the seeds sown in the spring season will grow luxuriantly and the plants will mature and flower at normal time. The process by which temperature range of plant is lowered in order to get early crop is called *vernalization*. This practice is very common in cold countries.

Temperature determines the growth of many plants. Cotton prefers high temperature. Potato gives highest yield in low summer temperature. Growth of plants is retarded at high temperatures.

Temperature in combination with humidity and other factors helps in the spread of diseases in plants. Low temperature and high humidity favour the rust attack. Low temperature, high humidity and cloudy weather favours the damping off, seedling blight, food rot and root rot diseases of cucurbits, tobacco, papaya and ginger.

Temperature varies from place to place and likewise the vegetations of different areas also differ considerably. Desert plants grow in extreme heat, aquatic plants grow in low temperature range, and grasses prefer to grow in the area of moderate temperature.

Temperature in combination with moisture determines the general distribution of vegetation. Northern, southern, tropical and temperate vegetations depend solely upon temperature and moisture.

Precipitation and Atmospheric Humidity

Water is one of the most important climatic factors. It affects the vital processes of all the living beings. It is the plenary agent

that sets in motion the nutrients of the soil and makes them available to plants. It affects the morphology and physiology of the plants. It, in combination with other factors, regulates the structure and distribution of plant communities.

In nature, water may be found in vapour, liquid and snow or ice states. In the atmosphere, water is found in the form of vapour. The quantity of water retained in the atmosphere depends on temperature and wind. Vapour increases in the atmosphere if the temperature rises and pressure decreases. At certain temperature and pressure, the maximum water-laden air is called saturated atmosphere. At saturation point, if the temperature is lowered the water holding capacity of atmosphere is reduced which causes the condensation of water vapour in the form of rain drop, dew, frost, sleet, snow, etc. This is *precipitation.*

The water vapour present in unit volume of air is called *absolute humidity*. This is expressed in terms of percentages of water vapour present in unit volume air at certain temperature. The amount of water required to saturate the same unit volume of air under constant physical conditions is called *relative humidity*.

Water of atmosphere reaches to the earth's surface through precipitation and from earth's surface it reaches to the atmosphere through evaporation and transpiration (Fig. 2.1). Thus a continuous

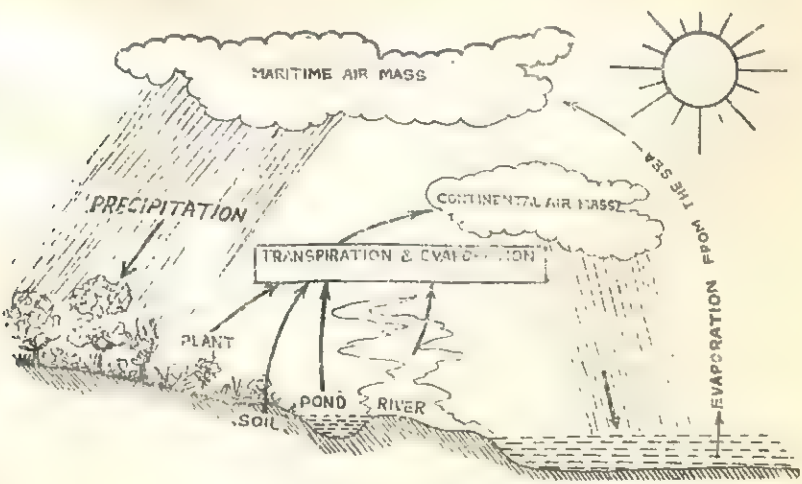


Fig. 2.1—Hydrologic cycle in nature.

circulation of water from earth to atmosphere and *vice versa* is maintained in nature. This is called *water cycle* or *hydrologic cycle*. It has been estimated that about 80,000 cubic miles of water from the

oceans and 1,500 cubic miles of water from lakes and land surface evaporates annually. The total evaporation is equalled by total precipitation (of which about 24,000 cubic miles of water falls on land surface). The main source of water for terrestrial plants is rain water. Penck using precipitation-evaporation ratio, has classified the climate as follows :

(i) *Arid* —It is characterised by the condition that evaporation is greater than precipitation.

(ii) *Arid-humid*—When evaporation is more or less equal to precipitation.

(iii) *Humid* —When evaporation is lesser than precipitation.

The total rainfall, especially the distribution of rainfall throughout the year is one of the leading features of climate. Rainfall map of the world corresponds very closely with the distribution of great vegetational zones in the world.

Sudden and heavy rains are not so beneficial as are moderate and continuous rain because in the heavy rain a large amount of water is lost from the surface of soil as run off and the soil is eroded.

Rainfall is determined largely by geography and pattern of large air movements of weather systems. When the moisture-laden winds blow from the oceans towards the high mountain they deposit most of the moisture on the ocean-facing mountain slopes with a resulting 'rain shadow', and produce desert on the other side. The higher the mountain the greater is the precipitation of moisture over it. This is the main reason why deserts are usually found behind high mountains. The deserts are also found along the sea coasts, where wind blows from large interior dryland areas rather than off the ocean.

The amount of rainfall in different localities largely determines the nature of vegetation therein. The following tabulation gives a rough idea about the plant communities that may be expected in regions with different amounts of annual rainfall.

Annual rainfall	Vegetation
1. 0 to 13.24 cm	Desert
2. 13.25—35.1 cm	Semiarid grass land
3. 35.2—63.5 cm	Dry, subtropical grass land, savanna (a grass land with scat-

Annual rainfall	Vegetation
	tered tree or scatter clumps of trees—a community type intermediate between grass land and forest) open wood land
4. 63.6—114.3 cm	Humid subtropical forest
5. 114.4—203.2 cm	Tropical rain forest

Snow, which may lie on the ground to form a valuable protective blanket and also a reserve of water, is apt to limit the growing season by its late melting.

Hail, a special type of precipitation during the summer season in the form of small ice pieces, may cause serious injuries, especially to young crops.

Dew and sleets make a very vital contribution to precipitation in the regions of low rainfall. Dew and ground fog may be important to plants not only in coastal forest but also in deserts near the sea coasts where they provide much of surface water on which the ephemeral plants depend.

The atmospheric humidity influences directly the form and structure of the plants. It directly affects the transpiration rate of the plants. In dry atmosphere transpiration rate increases and as a result of this the water content of the leaf tissues decreases and the leaves wilt temporarily. Water requirements of different plant species differ considerably. Some species on one extreme, thrive well in the region with an annual precipitation of 10 cm while some, on the other extreme, grow only when they are submerged in water. On the basis of their water requirements, the plants are grouped into three ecological groups :

(*i*) *Hydrophytes.* Plants adapted to aquatic environment.

(*ii*) *Xerophytes.* Plants adapted to grow in dry lands where water content is low.

(*iii*) *Mesophytes.* Plants living in the habitat that usually shows neither an excess nor a deficiency of water.

The actual effects of water on the plants may be complicated

by other conditions, such as temperature and atmospheric humidity. The combination of temperature and precipitation plays vital role in determining the broad features of plant distribution on the earth surface.

The temperature exerts more limiting effect on the organisms when the moisture conditions are exterme (*i.e.,* either very high or very low) than when such conditions are moderate. Likewise moisture also plays a more critical role in the extremes of temperature. Some modern climatologists taking into consideration the quantitative measures, effectiveness and seasonal distribution of moisture and temperature have classified the climate into temperature, tropical, polar and high altitude climates. The characteristic features of these climates and peculiar type of vegetations restricted to them are given in the following chart.

Climate	Characteristic features of climate	Vegetation
1. Temperate climate	Cold and moist with well marked seasonal and diurnal fluctuation, average annual rainfall more than 762 mm (30″), warmest month above 10°C	Luxuriant vegetation in favourable situation. Trees and shrubs dominant, and herbs exceeding trees and shrubs in number.
2. Tropical climate	Warm and widely humid with mean temperature of the coldest month usually 17.8°C and rainfall very heavy (200-400 cm per annum). Frost and snowfall are usually unknown. Little or no seasonal variation.	World's luxuriant rain forests in the regions of high rainfall. Shrubs, grass land, desert community in the regions of decreasing rainfall.
3. Monsoon area.	It is characterised by dry and wet seasons. Rainfall very heavy.	Deciduous trees and shrubs.
4. Climates of polar regions	Warmest month below 10°C. Precipitation mostly in the form of snow	Vegetation mostly low and scant. Dwarf shrubs and grasses dominant.

Climate	Characteristic features of climate	Vegetation
and high altitudes.	and widely distributed. Annual rainfall less than 254 mm (10″). Owing to low temperature the relative humidity is high and evaporation rate is low. In the regions of high altitudes there is continuous light in summer and darkness in winter.	Mosses and lichens are common.

WIND

Air moves from high pressure to low pressure, causing wind. The atmospheric air consists of a number of grass particles and other constituents. The proportion of grass in atmospheric air is kept constant to a fair degree :

Nitrogen	78%
Oxygen	21%
Carbon dioxide	0·03%
Argon and other gases	0·93%

The other constituents vary depending upon habitat condition. They include water vapour, smelter gases, dust and smoke particles, micro organisms carried on these particles, pollen grains and spores etc.

The effects of wind on the vegetation are important. The wind exerts an influence upon both configuration and distribution of plants. It commonly affects other ecological factors, as for example, the water content and temperature in a given area, through its effect on evaporation. It plays both positive and negative roles in the atmosphere, for instance, it has drying effect upon soil and may occasionally act in opposite direction bringing in moist air that reduces the transpiration and evaporation and may actually lead to the deposition and precipitation of moisture. The following are the important effects of wind on vegetation :

(*i*) Wind increases the water loss by constantly removing the air saturated with water vapour from the intercellular spaces of the leaves and bringing unsaturated air in contact with leaves and young shoots.

(*ii*) Mechanically, wind causes erosion of soil and abrasion of vegetation through removal of particles and physiologically, it decreases the growth of plants by way of reducing the moisture content of air and reducing the turgidity of plants on which it impinges. Moist air promotes the growth of mesophytes.

(*iii*) In strong dry and hot winds, young parts of plants may become shrivelled and killed in a few hours and the surface of soil may become dry.

(*iv*) In open situations, *e.g.*, sea shores and high mountain tops, where the strong winds blow all the year round in one direction, the trunks and branches are twisted chiefly in the direction, of prevailing wind. In such plants generally the growth of buds becomes checked on windward side (Fig. 2.2).

Fig. 2·2—Figure shows the effect of abrasive ice particles and strong wind on the branch growth. The buds on the windward side are either killed or they grow opposite windward side.

(*v*) In strong wind, big trees are uprooted and small plants and grasses are affected but to a very little extent. By strong wind weak plants like wheat, maize, sugarcane, jwar, etc. are bent against

the ground. These prostrated plants, if their stems are not too mature, may again become partially erect. This is due to differential growth at the meristematic lower nodes of these plants.

(*vi*) Wind is an important agent for the dispersal of pollen grains, fruits, seeds and spores of the plants. In deserts, the strong wind carries the sand and seeds. Thus, it plays important role in local distribution of plant species or communities of plants. Some types are wind resistant but some may be totally dependent on wind for their dispersal. Many plants are unable to flourish or even exist in the exposed situations if they are brought to such places by wind. Strong wind causes injuries to plants growing at high altitudes. In desert, the storm results in big sand-dunes which cover the vegetation (Fig. 2.3)

Fig. 2.3—A view of sand dunes in the desert.

(*vii*) In the areas subjected to strong winds, the leaves of plants become small and rolled. The transverse section of stem shows eccentrically developed secondary wood, *i.e.*, the diameter of the trunks in the direction of wind becomes greater than that at right angle to it. The plants in such areas show extensive development of mechanical tissues which provide mechanical support and save the plants from wind injuries.

In Indian and many other countries of the world, unchecked winds have caused total disappearance of vegetation at certain places and rendered big areas deserted. Rajasthan desert in India is spreading eastward due to unchecked wind erosion.

EDAPHIC FACTORS OR SOIL FACTORS

Edaphic factors are those which are dependent on the soil as such—on soil constitution, soil water, soil air, soil organisms and so

forth. Soils at different places vary considerably in their structure, components and properties. These differences in the soils are often largely responsible for differences in vegetation within the same climatic region, consequently they are of great significance in the distribution of plant communities.

Soil is defined as the unconsolidated top or superficial layer of earth's crust lying below any aerial vegetation and undecomposed dead organic remains, and extending down to the limits to which it affects the plants growing about its surface. Beneath the soil, lie the subsoil and unweathered rocks.

Soils commonly become stratified into layers or horizons, at different depths. The layers of soil at different depths show different compositions and natures. Normally three main horizons or groups of horizons can be recognised. These are the upper horizon or *A* horizon, the middle horizon or *B* zone and *C* horizon (Fig. 2.4). These horizons are often divided by the use of appropriate subscripts, such as A_1, A_2, A_3. *A* horizon or surface soil designates the top stratum which is subjected to marked leaching. It is a layer of greatest biological concern as the plant roots, small animals, and microflora and fauna are found here most densely. In this zone the concentration of the organic matter is highest, hence it is the dominant reservoir for plant nutrients.

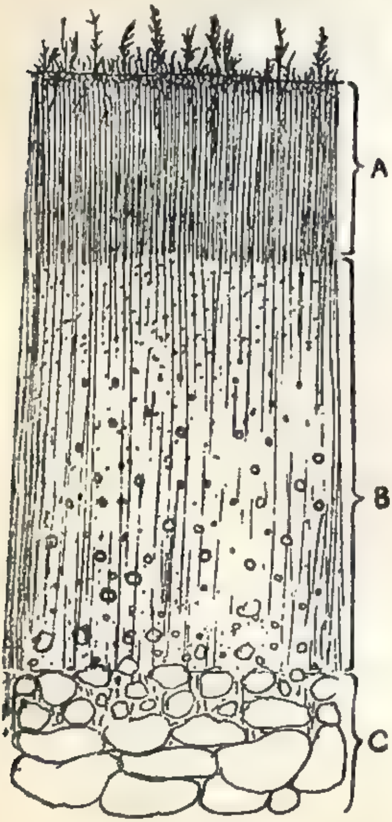


Fig. 2.4—Soil profile showing different horizons.

The *B* horizon or the subsoil lying under *A* horizon has little organic matter, very few plant roots—and a sparse microflora and fauna. In it, iron and aluminium compounds are often accumulated. *A* and *B* horizons collectively represent the true soil. At the bottom of profile is the *C* horizon which contains the parent materials of the soil. In this layer the organic matters are present in small

amounts and little or no life is noted. The essential components of most garden soils are as follows:

(*i*) Mineral particles (obtained by weathering or breakdown of the rocks) of variable size—40—50% by volume and 95% by weight ;

(*ii*) Soil water—5.30% ;

(*iii*) Soil air or soil atmosphere—25·30% ;

(*iv*) Organic matter or soil humus arising from the death and decay of plants or the parts of plants and animals are added as manures—1 to 5% by weight ;

(*v*) Soil organisms, including both soil flora and soil fauna, as for example, protozoa, nematodes, earthworms, bacteria, fungi, algae, etc. Fig. 2.4 A gives a rough idea about the percentage of various components of garden soil.

The important edaphic factors which affect the vegetation are as follows :

(*i*) Soil moisture ;
(*ii*) Soil reaction ;
(*iii*) Soil nutrients ;
(*iv*) Soil temperature ;
(*v*) Soil aeriation or soil atmosphere ; and
(*vi*) Biotic components of the soil.

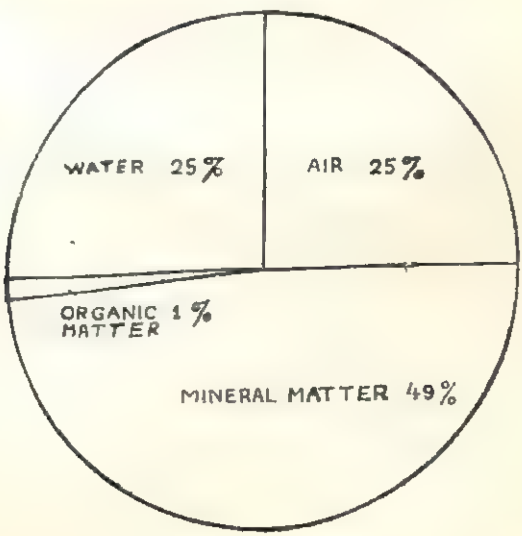


Fig. 2·4 A—Soil components.

(i) Soil moisture. Plants absorb a small quantity of rain water and dew directly but a large quantity of water they take from

the soil. Water held in the soil is found in the following forms (Fig. 2.5).

(*i*) Gravitation at water
(*ii*) Capillary water
(*iii*) Hygroscopic water
(*iv*) Water vapour
(*v*) Combined water.

Gravitational water is free water which percolates downwardly through the pore spaces between soil particles and is accumulated in the pore spaces in the form of *ground water*. The amount of water present around the soil particles and held by surface tension and

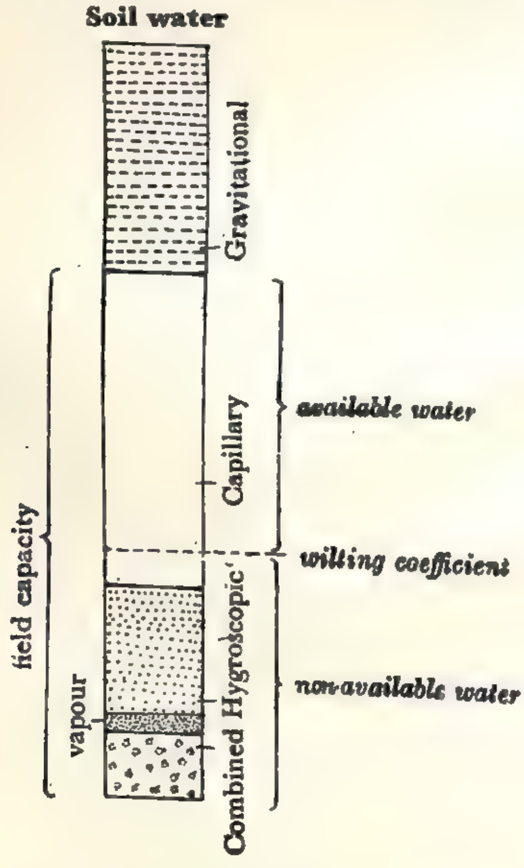


Fig. 2·5—Soil water.

attraction force of water molecules is called *capillary water*. Capillary water remains readily available to the roots up to a certain soil moisture tension. Water which is absorbed on the soil particles and held on the surface of particles by forces of attraction and cohesion

of its molecule is called *hygroscopic water.* This is the moisture remaining in air-dry soil. It cannot be used by the plants. The soil atmosphere, like external atmosphere, also contains moisture in the form of *water vapour.* Water of chemical compounds is called *combined water.* Total water content of the soil is called *holard.* Water of the soil which is easily available to the plant is termed as *chresard* and water which is so strongly held by the particles as to be unavailable to the plants is termed as *echard.* The availability of soil moisture is influenced by many conditions, such as distance of water table from the soil surface, the rate at which water percolates downwards, the sizes of soil particles, the amount of annual rainfall and other precipitation, and the distribution of precipitation throughout the year. Water tends to promote the stratification of soil. Soil's available water is the chief factor responsible for local difference between plant communities. Heavily water logged soil is injurious for the growing plants because heavy accumulation of water in the soil reduces the soil aeration. Low water content in the soil is also injurious because it causes either temporary or permanent wilting of plants. Soil water is not only important in connection with direct fulfilment of water requirements of plant but it is also the medium by which mineral salts essential in the nutrition enter the plants in dissolved state.

(ii) Soil reaction. This edaphic factor influences the growth and distribution of the plants. The soil may show acidic, alkaline, or neutral reaction. The growth and productivity of many species or plants are critically, related to soil acidity. Species of *Rhododendron,* Cranberris are acid loving. Most of the field crops, such as barley, maize, soybeans, tomato, rye, potato, flourish in slightly acidic soils. Many ferns and beech trees thrive best in slightly alkaline soils. Soil acidity is important in many ways; in the behaviour of soil solutes, and in the relation of roots to the soil. Soil acidity affects the availability of iron manganese, phosphate, and other ions. In the acid soils, iron and manganese are available in appreciable quantities, but in the neutral or alkaline soil they are available in meagre quantities to green plants. The accumulation of calcium, sodium and magnesium salt in the soil results in alkalinity. The reaction of soil influences the absorption of water and soil solutes by roots through its direct effect on inhibition and permeability of root cell membranes.

(iii) Soil nutrients. The nature and availability of soil solutes are fundamentally important from the standpoint of plant nutrition. Normally, inorganic solutes are absorbed by the plants

in the ionic forms. Different species of plants, no doubt they require the same ions for their normal development, require them in varying quantities. In saline soil where the percentage of salts in soil solution is high only halophytes (salt-loving plants) grow. Some plants require lime and grow in calcium rich soils. Such plants are called *calcicoles* or *calciphytes*. Some plants do not thrive well when they grow in calcium rich soil. These species are called *calcifuges* or *oxylophytes*.

Humus, a dark amorphous substance formed by partial degradation of dead organic remains is an important source of mineral and organic nutrients of plants. The fertility of soil is usually correlated with its humus content. Humus is the main source of nutrients for soil micro-organisms and green plants.

(iv) Soil temperature. Soil temperature in combination with other edaphic factors influences the properties of soil itself and plants as well. Low temperature reduces the rate of water and solute absorption by roots. Root injury due to low temperature in the winter is more common in sandy soil than in clay. Soil temperature is also important in the sense that it plays important role in determining the geographical distribution of plants on the earth. Soil temperature is affected by air temperature, the intensity of sunlight, the angles at which sun rays strike, on the surface of soil, daily duration of sunlight, the amount of soil moisture and many other factors.

(v) Soil atmosphere. In the soil, the spaces left between soil particles are called pore spaces. These spaces contain air. Soil air contains slightly lower proportion of oxygen and higher one of CO_2 than atmospheric air contains. Waterlogged soils are deficient in oxygen. Normally, plenty of oxygen in the soil is necessary for the life of micro-organisms and other soil inhabitants. It is also necessary in the respiration of underground parts of higher plants. Oxygen content of the soil is also an important factor in seed germination. The germinating seeds respire rapidly and usually they require large amount of oxygen.

(vi) Soil organisms. The plants, animals and microbes inhabiting the soils show marked effects on the soil fertility. Decomposing agents, such as, bacteria, fungi, and many others convert dead organic matters into humus, free organic compounds and organic ions and thus make the nutrients available to the plants. Some soil organisms secrete essential or beneficial substances includong growth hormones and some of them secrete toxic substances in

the soil, which show marked effects on the growth and distribution of plants. Some of the bluegreen algae like *Nostoc, Anabaena, Cylindrospermum* are beneficial to the higher plants because they fix atmospheric nitrogen into nitrogenous compounds that are utilised by the higher plants. Singh (1961) found that algal films that developed on paddy fields in Uttar Pradesh and Bihar were active nitrogen fixer bluegreen algae. The animals of burrowing habitat also play important role in the soil by turning over the soil. Earthworms increase the fertility of the soil by adding excretory matters to it and also by making it loose. Local distribution of plant communities in different regions also brings about changes in the composition and fertility of the soil in those regions.

BIOTIC FACTORS

The biotic factors include the influence of living organisms, both plants and animals, upon the vegetation. Any activity of the living organism which may cause marked effects upon vegetation in any way is referred to as **biotic effect**. The biotic effect may be both direct and indirect. It may be beneficial for the plants in some respects but detrimental in other respects.

The plants live together in a community and influence one another. In the forest there are many plant communities, such as trees, herbs, shrubs, mosses, lichens. These communities interact with one another and adjust according to environmental conditions. Trees cast their shadow on many shade-loving plants which grow around or beneath them. The micro-organisms, such as bacteria, algae, fungi and viruses affect the life of plants of a given area in many ways. Besides these, the decomposition of dead parts of dead plant bodies causes significant addition of organic compounds and humus to soil. In this way, the vegetation modifies the habitat to a considerable extent. Similarly, animals which are in close association with plants also affect the plant life in one or several ways. Many animals, use plants as their food and for shelter as well. Besides the animals, the man is the most significant agent for modifying the vegetation.

The biotic effects modifying the vegetation can be discussed in the following heads:

(1) Interactions between the plants and local animals and man.

(2) Interaction between plants growing in a community.

(3) Interaction between plants and soil micro-organisms.

1. Interaction between plants and Local animals and man

These can be described under the following heads:

(*i*) Effects of grazing and browsing by animals.
(*ii*) Role of animals in the pollination.
(*iii*) Role of animals in the dispersal of seeds and fruits.
(*iv*) Insects and carnivorous plants.
(*v*) Effects of human activities on vegetation.
(*vi*) Myremecophily.
(*vii*) Miscellaneous effects.

(i) Effects of grazing and Browsing. *Grazing* means eating away of unharvested herbs as forage by animals as for example, eating away of grasses by goats, whereas *browsing* refers to a similar use of shrubs or trees by animals (Fig. 2.6), as for example, eating away of leaves and small twigs of Margosa (Neem) by camels. The animals destroy a large part of vegetation by grazing and browsing.

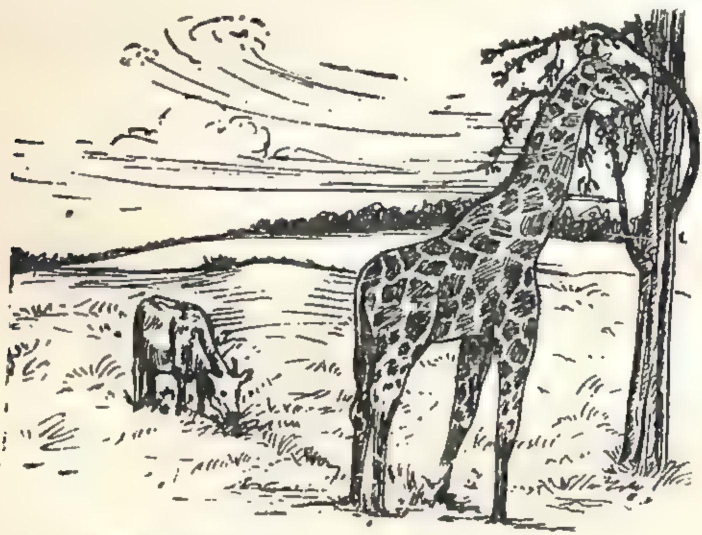


Fig. 2.6—Grazing and Browsing by animals.

Various other effects of grazing and browsing are summarised briefly in the following points:

(*a*) The grazing and browsing adversely affect the aeration of soil and make it compact and hard and finally render the soil unfit for the growth of trees and shrubs. Forests open to cattle are changed first into shrubby vegetations and finally into grasslands. Excessive grazing and browsing may thus change the pattern of vegetation and finally lead the area to develop into desert. Murphy (1951) is of the opinion that Sahara desert developed as a result of

unchecked and excessive grazing by goats, sheep and by introduction of camels in the area.

(*b*) The grazing and browsing reduce greatly the frequency of photosynthetic organs (leaves and apical green parts of stem) and thus curtail the assimilation.

(*c*) The grazing and browsing reduce the vegetation from the surface of earth to a considerable extent and thus expose the soil for erosion.

(*d*) The most important effect of grazing and browsing is the trampling. In the trampling complete destruction of small and weak annual herbs is caused by the hoofs, paws and feet of animals.

(*e*) In grazed pasture and meadows, dung avoiding plants (coprophobic plants) disappear giving place for the colonization of non-coprophilous vegetation.

(ii) Role of animals in pollination. A large number of plants depend on insects, birds and a number of animals for their pollination. These plants develop coloured flowers. The flowers possess scents, nectar, sap, edible pollens and many other characteristic structures for attracting insects towards them. Insects, birds and other pollinators visit to the flowers in search of honey and edible pollens. Flowers in the families Rosaceae. Compositae, Leguminosae, Rutaceae, Umbelliferae, Euphorbiaceae, Cruciferae, Ranunculaceae are pollinated by insects. Some plants are specialized in their pollination by particular type of animals, for example, *Rafflesia* is pollinated by elephants and birds, bilipped flowers of *Salvia* are pollinated by bees, entomophilous flowers of orchids, *Ficus* and *Calotropis* are pollinated characteristically by insects. It is observed that different types of flowers and their pollinators generally live together in the same biotic communities and affect each other's life.

Besides insects, birds, bats and some other animals, man too is taking active part in pollinating artificially one plant with the pollen of some other plant species. The artificial pollination is being used by man for the production of high yielding and disease resistant plant varieties.

(iii) Role of animals in the dispersal of fruits and seeds. Many animals, such as birds, bats, monkeys, act as important agents for disseminating the seeds, fruits and spores and thus they play important role in the migration of plants.

The seeds of many plants are very hard. Such seeds along

with fleshy parts of fruits are swallowed by animals. While passing through the alimentary canals of animals hard seeds are not affected by digestive juices. When the animals leave faecal matter, the uninjured seeds present in it germinate. Passing of feeds through the digestive tracts sometimes facilitates their germination in certain cases. The seeds of tomato, tobacco, guava and many other plants are dispersed in this way.

The hairy, spiny, hooked and sticky fruits and seeds of some plants get entangled with the bodies of birds and other animals and with the clothes of man and are brought to distant places. When the animals sit and clean their bodies at some places these seeds are dropped down there. Seeds and fruits of *Xanthium*, *Andropogon*, *Plumbago*, *Aegle marmelos* are dispersed in this way.

Ants are good agents for transporting oily seeds and small grains of cereals.

(iv) Insects and Carnivorous plants. Semi-autotrophic insectivorous plants, as for example, pitcher plant, *Drosera*, *Aldrovanda*, *Dionaea* bladderwort, etc. grow in the habitats which are deficient in nitrogenous compounds. These plants have some

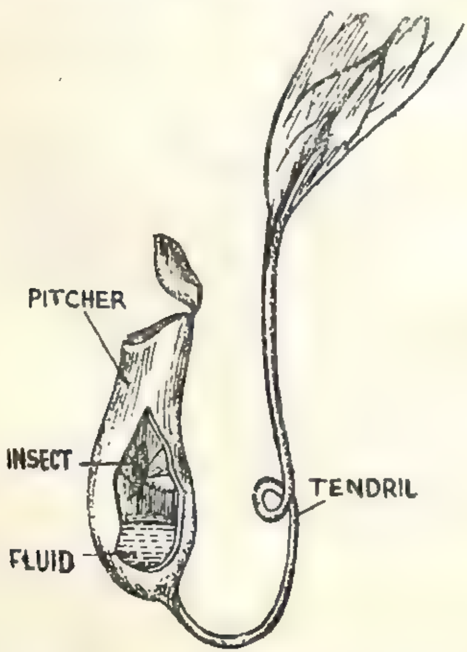


Fig. 2.7—Pitcher plant. A leaf pitcher with insect.

specialised organs and mechanisms for trapping and assimilating the preys.

Pitcher plants have leaf pitchers containing liquid and enzymes inside (Fig. 2.7). When the insects are trapped down in the pitcher they are digested and assimilated by it. In *Drosera* spathulate leaves are covered with sensitive glandular hairs which shine in the sunlight and attract insects and small flies. When the insects are entangled in the surface glandular hairs of leaves, digestive enzymes are secreted immediately which kill and digest the bodies of insects. The digested parts of insects are absorbed by the surface cells of the leaves.

Utricularia (Bladderwort) is an aquatic insectivorous plant which is commonly found in ponds of India. Its bladders catch and digest small swimming aquatic animals (Fig. 2.8).

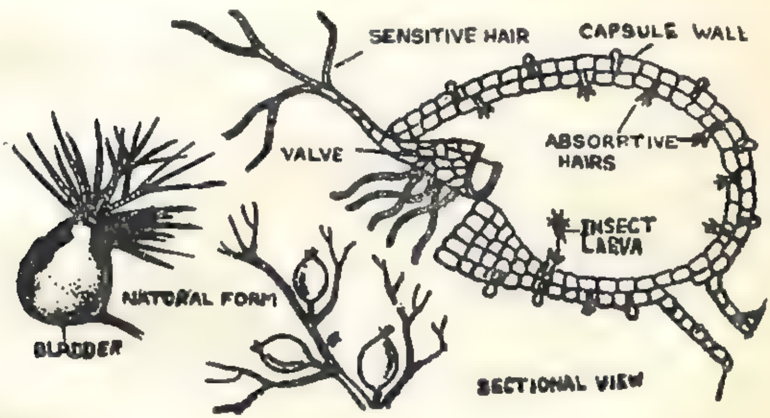


Fig. 2.8—*Utricularia*

(v) Effects of human activities on vegetation. Man affects vegetation in the following ways :

(*a*) By cutting, felling and replanting the forest trees.

(*b*) **Cultivation.** Besides the old methods of cultivation, man has adopted a number of advanced methods for cultivation of plants. Cutting, budding, grafting and other methods used by man are proved beneficial for certain plants. Now at various research stations men are performing cross-breeding experiments to evolve new varieties of plants that give high yields and are disease-resistant. In cultivation, the destruction of weeds by man eliminates the competition among the plants. Proper spacing of plants during cultivation also checks the competition among them for food.

(*c*) **Fire.** Fire is a biological factor rather than a physical factor because it is mostly caused by man's activity. Lightning

initiated fires have destroyed plants and animals since their early appearance on earth. In some countries, especially America and Africa, a lot of work has been done on the effects of fire on different ecosystems. A large body of information has developed on the effects of fire on grasslands and forests as well as on the use of fire in land management. The branch of ecology which deals with the effects of the fire on ecosystem is called "Fire ecology" or Ecopyrology. Plants having ability to withstand fire with little or no damage are referred to as *Pyrophytes*. A number of pyrophytes are known to occur in Siwalik hills. Important examples of pyrophytes are *Cochlospermum religiosa, Combretum nanum, Grewia sapida* etc.

(*d*) Man also clears the vegetation for making houses, roads, etc.

(*e*) In ancient times many human invasions took place in India which caused great destruction of vegetation. Alexander (330 B.C.), Muslim invasion after 850 A.D., Gori and Gaznavi, and Rajput invasions destroyed dense forests and converted them into deserts. Mohenjodaro and Harappa are examples which are supposed to have become deserted as a result of human invasion. The excavations of Mohanjodaro and Harappa indicate that shrubby plants were abundant in the desert areas of Punjab and Sind.

(vi) **Myremecophily**. Sometimes ants take their abode or shelter on some trees such as Mango, Litchi, Jamun, South American *Acacia* (*Acacia sphaerocephala*) (Fig. 2·9.) and so on. These ants act

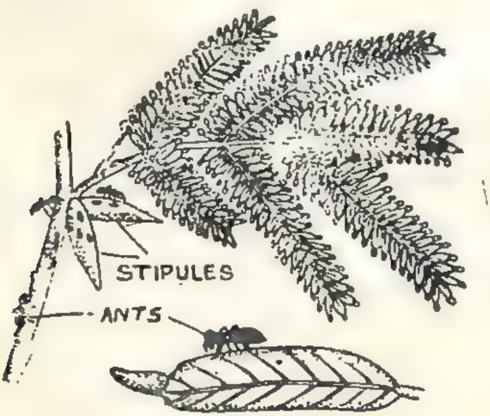


Fig. 2·9—Myremecophily.

as body guards of the plants against any disturbing agent. In lieu of this defence, the plants provide food and shelter to these ants. This phenomenon is known as myremecophily.

(vii) Miscellaneous effects. The animals also affect the plant life in many other ways. Some animals, as for example, back-eater, rodents, may kill a large number of trees. Juice sucking insects, woodpeckers, bud eating birds, sparrow, squirrel and other animals cause great harm to the vegetation. Elephants detach the branches of the trees and sometimes uproot the gigantic trees.

The insects, birds, squirrels, mice and rodents eat abundant seeds. Some animals eat and destroy seeds at the sowing time. Fishes, ducks and other aquatic animals depend upon aquatic plants for food and shelter.

2. Interactions between plants growing in a community

Various plants in the community react with one another in several ways for :

(*i*) Water,

(*ii*) Essential soil minerals and organic compound, and

(*iii*) Light and air.

The taller plants modify the habitat for the plants growing around and underneath them by casting shadow, protecting them from injuries by strong wind, by increasing the atmospheric humidity, and by determining the humus content of the soil.

The most interesting instances of interactions among plants growing in a community are as follows :

(*i*) Action of lianas ;

(*ii*) Effects of some epiphytes ;

(*iii*) Effects of parasitic plants.

(i) Action of lianas. Lianas are woody vascular plants growing on the ground, maintaining, more or less, autotrophic mode of life and growing upward taking support of some trees and other objects. The woody stems of these plants have well developed alternating vertical columns of secondary xylem and parenchymatous tissues which enable them to twist around the supporting objects (Fig. 2·13). In tropical evergreen forest, lianas grow at the top of the trees and form the top layer of the forest canopy. This habit enables these lianas to get

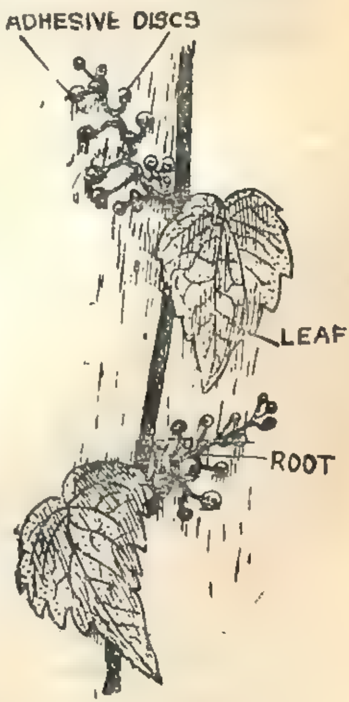


Fig. 2·10.—A liana

sufficient light. The lianas affect other plants also because they cast their shadow and check the light from reaching to the plants of lower storeys.

(ii) Effects of some epiphytes. The epiphytes grow on the leaves and stems of other plants. They are autotrophic and are dependent on other plants only for support. Epiphytes differ from parasites in not taking food from the hosts and also differ from lianas in not having any permanent connection with the soil. The examples of epiphytes may be found in the families Orchidaceae, Asclepiadaceae, Bromeliaceae, Cactaceae, etc. *Dischidia, Tillandsia* are most common examples. Epiphytes are found in humid climates. The two main problems for these plants are (*a*) maximum absorption of water from the atmosphere and from the bark surface of the supporting plant and (*b*) maximum economy in the water consumption. These plants develop two types of roots, namely the aerial and clinging roots. The aerial roots are thick and have specialised thin walled porous absorptive tissue, the 'velamen' on their surface. These roots absorb rain water and moisture from the atmosphere. The clinging roots fix the epiphytes on the surface of supporting plants. Because the epiphytes are autotrophic, they do not affect the supporting plants to any considerable extent.

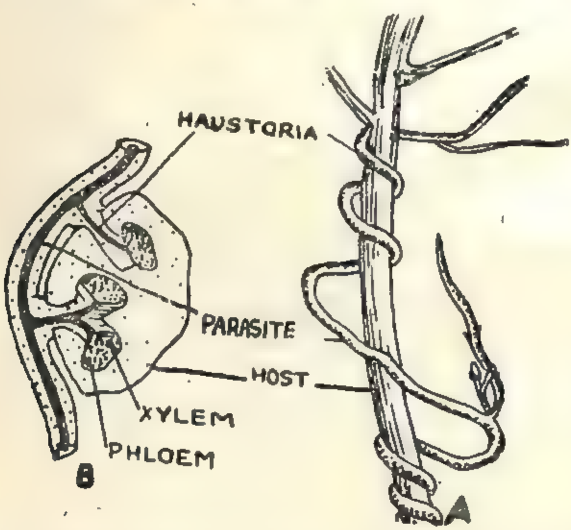


Fig. 2·14A—*Cuscuta* on the host. B—T.S. of host along with *Cuscuta*

(iii) Effects of parasitic plants. Some plants are heterotrophic and are dependent on other plants for their food requirements. They are called parasites. These are of the following two types :

(*i*) Ectoparasites (external); and
(*ii*) Endoparasites (internal).

The endoparasites are more destructive than the ectoparasites. Because the parasites take their food from host plants, they check the growth and ultimately cause the death of their hosts. *Cuscuta, Loranthus, Orobanche, Rafflesia,* and sandal wood tree (*Santalum album*) are important parasitic angiosperms which may grow either on roots or on stems and sometimes even on the leaves of the higher plants. The parasites may be either obligate or facultative.

Cuscuta (Fig. 2·11 A & B) is an obligate stem parasite on *Acacia, Zizyphus* and a number of other angiospermic plants. *Loranthus* is a partial stem parasite on Mango. *Orobanche* grows very commonly on the roots of crucifers and solanaceous plants as obligate root parasite (Fig. 2·12 A & B). Other important parasites

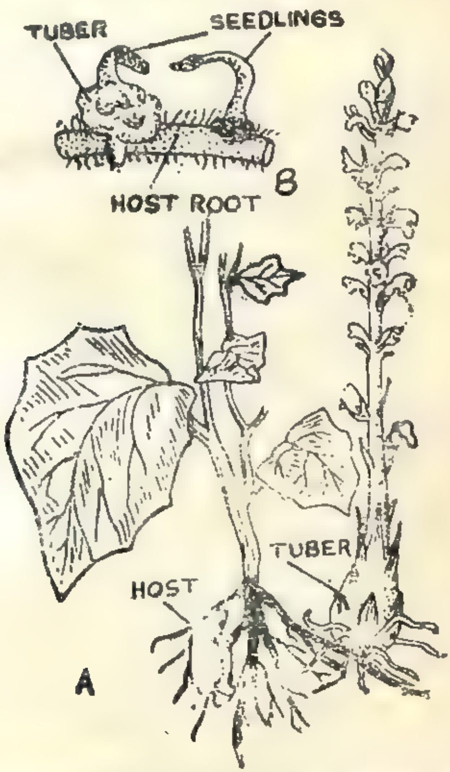


Fig. 2·12 A & B *Orobanche.* A—Parasite growing on the root of brinjal. B—A root of host with growing seedlings of parasite.

are *Rafflesia* on the roots of *Vitis* (Fig. 2·13), *Viscum album* on coniferous trees (Fig. 2·14). *Striga,* one of the smallest angiospermic parasites grows on the roots of Jawar *Arceuthobium minutissimum*, an

interesting smallest parasitic dicot, is an obligate stem parasite of *Pinus excelsa.*

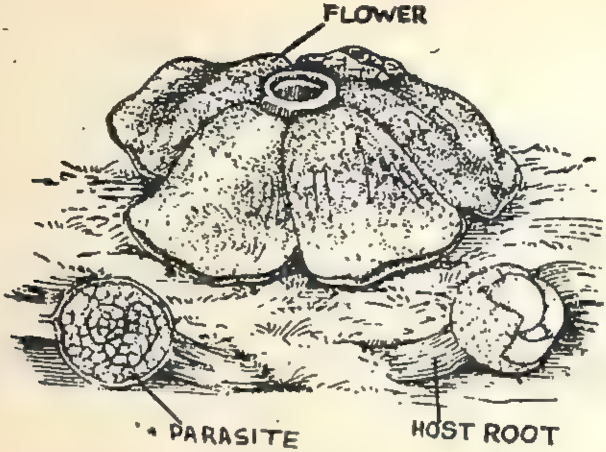


Fig. 2·13—*Rafflesia* on the root of *Vitis.*

Besides angiospermic parasites, fungi and bacteria are also known to parasitise plants and cause several destructive diseases in them.

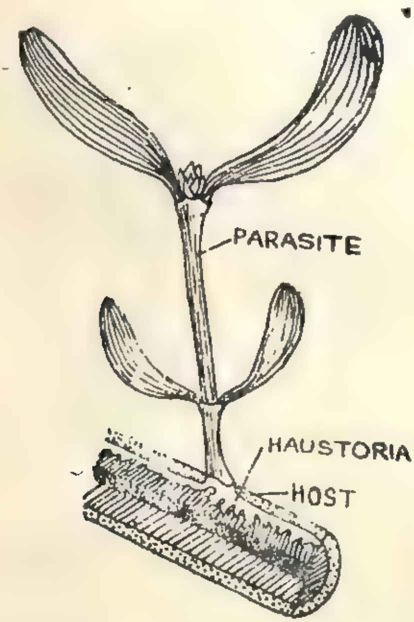


Fig. 2·14—Mistletoe (*Viscum*), a partial stem-parasite

Puccinia graminis is a parasitic fungus causing rust diseases in

wheat. Mildews, smuts, white rust, damping off, and blight diseases are generally caused by parasitic fungi.

Many algae are also known to parasitise several plants and cause diseases in them. Most common example is *Cephaleuros* which is found on a number of angiosperms.

3. Interaction between plants and micro-organisms

Various kinds of bacteria, protozoa, algae, fungi, worms, nematodes and other soil microbes act as important agents which alter the physical and chemical properties of the soils, increase or decrease their fertility. These changes in the soil properties have great impact on the nature and growth of vegetation. Very often soil microbes such as nematodes, bacteria and fungi cause many diseases in the underground parts of plants. Viruses too cause several mosaic and other diseases in many plants, as for exmaple, the curling of tomato leaves, mosaic patterns in papaya and lady's finger (Bhindi), bean mosaic, tobacco mosaic etc.

Some microbes secrete growth stimulating substances in the soil which induce the growth of plants.

Besides above effects, the soil microorganisms show symbiotic activities and many soil fungi form mycorrhizal association with the roots of higher plants. These two phenomena, *i.e.*, symbiosis and mycorrhizal associations, are described below.

Symbiotic influence. Some soil microbes live in close association with plants, both benefiting from each other. In this assoociation both the organisms are interdependent and they do not harm each other. This mutual relationship between two organisms is known as symbiosis and the interdependent organisms are called symbionts.

Many cases of symbiosis in plants are known. The nodulated roots of legumes contain nitrifying bacteria (*Rhizobium*) (Fig. 2·15). These bacteria fix atmospheric nitrogen into nitrogenous compounds and benefit the legumes by supplying nitrogenous compounds in usable form. The leguminous plants in return provide nutrients, water and shelter to bacteria. When the roots of these plants die, decomposition of dead remains takes place in which the nitrogenous substances are converted into nitrite, nitrate and ammonium ions that are absorbed by the plants. *Nostoc* and *Anabaena* living symbiotically in the coralloid roots of *Cycas* also fix atmospheric nitrogen.

Lichens also show symbiosis. These are synthetic plants in which algae and fungi live symbiotically. Generally, the algal component belongs to myxophyceae and fungal components are ascomy-

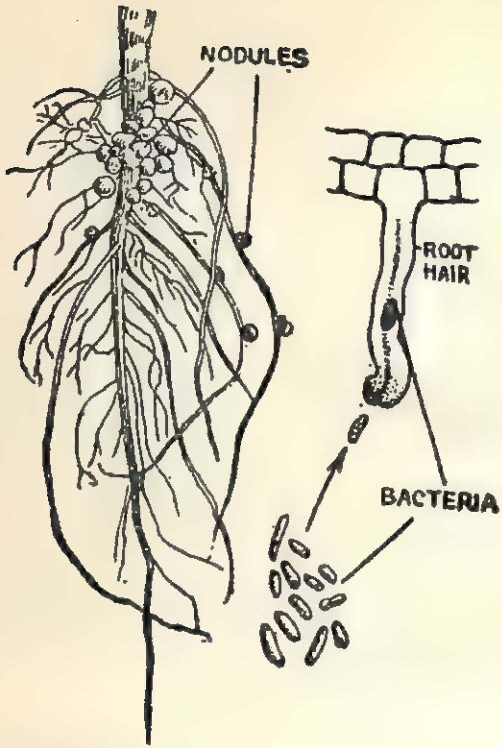


Fig. 2·15 – A nodulated root, soil bacteria and infected root hair

cetous or sometimes basidiomycetous forms. In this association, algal component fixes the atmospheric nitrogen, prepares food and supplies nutrients to its fungal counterpart. Fungal component gives support to the algal component. It also saves algae from desiccation because of its sponginess and high water holding capacity.

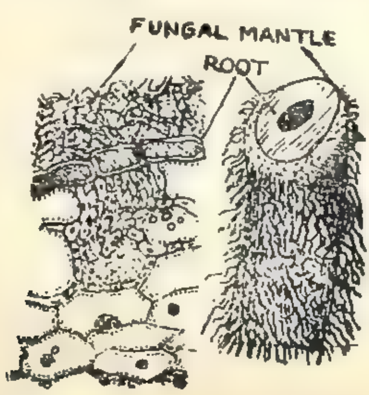


Fig. 2·16 –

Mycorrhizal association. Sometimes fungi grow on the surface or inside the roots of higher plants. They are called mycorrhizae. Micorrhizae are of two types.

(*i*) *Ectotrophic mycorrhiza*. Fungus lives on the surface of roots of higher plants (Fig. 2·16).

(*ii*) *Endotrophic mycorrhiza*. Fungus penetrates the deeper tissues of the roots and rhizomes (Fig. 2·17).

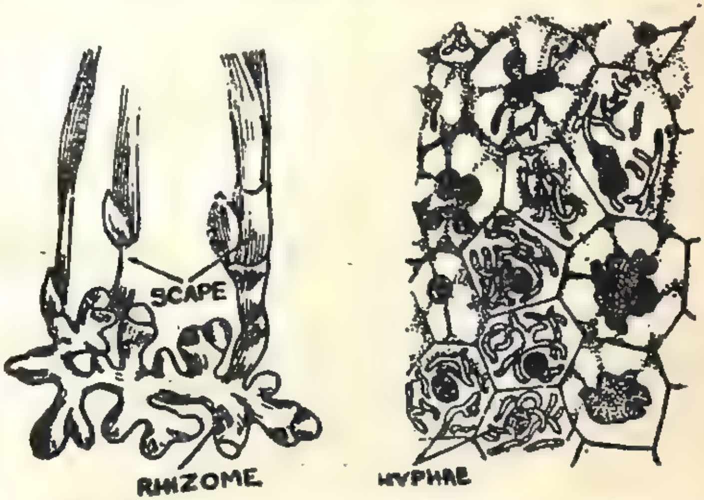


Fig. 2·17—A swollen rhizome with endophytic mycorrhiza

The roots with mycorrhizae are unbranched and without root-caps and root hairs. Fungal hyphae in this association act like root hairs, absorb water and minerals from the soil and supply them to the roots. The roots in return provide food and shelter to these mycorrhizae. Blue berries can not grow without mycorrhiza. Orchid seedings do not develop properly unless they become infected with mycorrhizae.

Recent researches have shown that mycorrhizae play very important role in the root tissue. They regulate acidity and sugar content in the root tissues and enable the roots to grow vigorously.

QUESTIONS

1. What is environment ? What are various environmental factors which influence the plant life ?
2. What is the effect of light on vegetation ? What is its significance to plants ?
3. What is the effect of biological factors on plants ?
4. Write short notes on :
   Biotic factors, Mycorrhiza, Soil profile, Soil water, Effect of wind on vegetation.

3

SOIL EROSION AND CONSERVATION

Living organisms directly or indirectly depend upon soil for their existence. Life will vanish if upper half a meter depth of earth's crust is removed. Its importance for plant life is still the more. Soil is the medium for root growth, source of food and water. The soil has its own life history. It is born, matured and lost. Soil is born out of rocks and it matures under the influence of climatic factors mainly precipitation and temperature. Under the moist cold climatic condition weathering is called "**Gleization**" which results in the development of Tundra soils. There is present glei layer at the bottom of solum which is sticky compact and structureless. Its colour is generally blue-gray because of reduction of Iron compounds. In cool moist climates highly acidic soils of low fertility are developed under the weathering process of **podolization**. Acids are formed by slow decomposition of organic matter, which percolate with rain water. This in turn carries oxides of iron and aluminium to subsoil where these get precipitated. Silica remains in top soil because of its insolubility.

In moist warm climates the process of **laterization** results in the development of soil where iron and aluminium oxides remain on the surface while silicon being converted into silicic acid moves downward. The characteristic vegetation developed is Rain forest type. However at maturity agriculture is not possible in this type of soil unless fertilisers are constantly used.

In arid type of climate the rainfall is not so much as to remove away Calcium and Magnesium ions. Carbonates get accumulated

and colloidal aggregates are immobile. The process is called calcification.

It normally takes 200-800 years for the development of an inch layer of soil from the parent rock material. An inch of soil per acre weighs approximately 1524 quintals.

The soil is gradually displaced from its natural profile and this displacement of particles is called **Soil Erosion**. This displacement to the extent of about 30 quintals per acre per year is just equal to the soil developed from the parent rocks. This is called *Normal Erosion*. When the displacement is at a rapid rate than this the erosion is called as *accelerated erosion*. This accelerated erosion if not checked can wipe out the civilisation. The causes of erosion are natural such as Water, Wind and Gravity or Biotic *i.e.*, Man and Animals.

Types of Erosion :

(A) Erosion due to water

(*i*) **Rain drop or Splash Erosion**. It is due to the effect of falling rain drops. The effect is twofold. Firstly its impact disintegrates the soil particles which becoming finer are easily carried by the flowing water. Secondly the finer particles get into the interspaces resulting into the disturbance of soil pore space and thus air and moisture. Calculations have shown that 10 cm of rainfall in 2-3 hours duration would raise the 20 cm deep soil particles eighty-six times to a height of about 1 meter.

(*ii*) **Sheet Erosion**. The gradual and uniform peeling away of the soil surface by the action of flowing water is called Sheet erosion. The rain drops form a thin layer of water on the earth's surface, which flows along the slope carrying soil along with it. Along with soil humus and mineral nutrients are also carried and the soil is rendered infertile. Lower layers of the soil which are more susceptible to the erosion become directly exposed to the action of water, air, light and temperature. Water holding capacity of soil is adversely affected as the finer particles are carried away.

(*iii*) **Rill Erosion**. Slow movement of water along the slope results in formation of small channels which can be removed during agricultural operations. These are called as rills. Its effect is more visible on the lower side of slopes than on the upper slopes. The formation of rills should be checked immediately because their advanced stages are very dangerous.

(*iv*) **Gully Erosion**. Gullies are wider and deeper channels which cannot be made up by simple agricultural operations. These

may completely destroy land adjoining them. Since water flows with greater velocity in them they become wider and wider as time passes. On the sides of the rivers such gullies are called ravines. Streams also along their banks carry on such erosion.

(*v*) **Internal Erosions**. This may be defined as the displacement of upper particles of soil which are carried downward by the gravitational water. Depending upon the kind of soil it has useful or harmful effects. Soils which allow rapid percolation of water are adversely affected while those in which percolation takes place slowly the effects are useful. The nutrients are carried to the root zones for absorption. The subsoil becomes richer.

(*vi*) **Plus Erosion.** The waste material is brought about by flowing water and deposited over the fertile land affecting fertility of land.

(*vii*) **Land Slides or Slip Erosion**. Heavy rainfalls result in the bodily movement of great soil masses along the slopes. They are a common site in mountainous areas during the rainy seasons. Wrong agricultural practices add to this type of erosion in the hills where the farmers make slopy terraces facing the open side. Gravitational pull only further adds to this erosion because too wet soils on the slopes have poor stability.

(B) Frosion due to the Wind

Wind erosion is of 3 types :

(*i*) **Surface Creep**. Heavier particles move along the soil surface by the action of blowing wind. These particles vary in size from 0·5 to 1·0 mm.

(*ii*) **Suspension**. Soil particles less than 0·1 mm. get suspended in the air due to the blowing wind. These suspended particles are carried to long distances by wind storms. These dust storms commonly appear during summer days. These particles are the most important for consideration of higher base exchange capacity, greater water holding capacity, greater cohesion and adhesion, structure developing qualities and greater fertility value.

(*iii*) **Saltation**. The soil particles of sizes 0·1 to 0·15 m.m. are lifted vertically upwards being unable to form suspension strike back. Their bounces set in motion the other soil particles. Major portion of wind erosion is due to saltation.

50% of wind erosion is below 5 cm. of the ground level and about 90% of soil movement in Wind Erosion is below the height of 30 cms.

Factors which Favour Erosion :

(A) Climatic factors. Precipitation is the most important factor which favours erosion. The intensity, duration and frequency of rainfall will determine the loss of soil. The relationship is direct. Low rainfall for short duration may have no influence on soil erosion. The velocity of wind also has direct influence on wind erosion of soil. The greater the velocity more will be the erosion. Higher temperature will lead to dryness of soil particles which can be easily carried by blowing wind. At the same time there will be rapid rate of decomposition of organic matter at higher temperature and hence water holding capacity is adversely affected increasing the rate of erosion. In areas of lesser humidity loss of water due to evaporation from soil is more and its susceptibility to wind erosion is increased.

(B) Geographical or Topographic Factors. The degree and length of slope affect the soil loss due to water. The steeper the slope rapid is the loss of soil. If the velocity is doubled the carrying capacity becomes 64 times.

(C) Edaphic Factors. The texture, structure, depth and organic matter of soil affects soil losses. Heavy or alkaline soils are highly affected. The impermeable soil layer will aid erosion because of no percolation of water. Deeper soils have better growth of vegetation and thus get some protection.

(D) Biotic Factors. Man controls these in the form of land management practices. His efforts in right direction can save huge losses due to soil erosion. Better agricultural practices, judicious cropping patterns, controlled grazing, proper drainage etc. will reduce erosion. Soil covered by vegetation is always more safe than the naked soil.

Harmful Effects of Erosion :

(1) Decrease in the depth of soil results in the decrease of medium of root growth, water retaining capacity and nutrients for plants.

(2) Crop yields are poor as the soil fertility goes on decreasing.

(3) Soil air and moisture balance is disturbed because soil aggregates are broken down.

(4) The growth of soil microorganisms is adversely affected thus humification and mineralisation so essential for the fertility of the soil is adversely affected.

(5) Land development becomes uneconomical and difficult.

(6) The percolation of water into soil is decreased. Impermea-

ble layer being exposed, the rate of run off water is increased. The drainage becomes difficult.

(7) The quantity of organic matter in soil goes on decreasing. The humus is lost and addition of further material is decreased because of poor growth of vegetation in soil eroded areas.

(8) Water supply from rivers and streams becomes seasonal instead of remaining perennial. This is due to the fact that during dry periods flow of water into rivers is maintained by infiltrated water. As the soil erosion takes place the infiltratian of water is decreased *c.f.* 6 above.

(9) The eroded soil is deposited in the river basins. Their capacity is greatly reduced. During rainy seasons this results in the floods. The flooded areas have huge losses on account of land, crops, house, cattle and sometimes even lives.

(10) Soil conservation measures in the form of construction of dams, river valley projects etc. put heavy economic burden.

(11) Silting reduces the life of river valley and hydroelectric projects. In Ootacamund a reservoir built for power house having an average estimated life of 100 years was silted up in 19 years. The investment made for making provision of desilting is dead investment. Nearly 1/7th of the cost in Bhakra Dam is dead investment because of keeping provision for dead storage for sedimentation.

(12) For maintenance of canals silt clearance has to be done for which there is huge recurring expenditure.

(13) Fisheries cannot be successfully maintained in muddy waters.

(14) In plains specially along rivers and canals there arises a water logging problem which in turn results in alkalinity and salinity of soils. Their reclamation is difficult.

(15) Dredging (removal of mud) is a costly operation which has to be undertaken in the harbours located at the river mouths. Rivers deposit sediments in the sea harbours.

(16) The machines in the power houses need frequent replacements because of the effect of silt in water.

SOIL CONSERVATION

It may be defined as the most efficient way of soil and water management so as to have maximum crop yields. Anti-erosion measures such as grass or tree planting or engineering works undertaken in areas which were visibly affected by erosion were used to be taken till the problem of soil erosion was deeply probed. The

problem revealed that it is not only soil management which is needed but also the water management. It was felt that the soil erosion can be checked out only by a well planned judiciously worked out system of land and water management and that was named as soil and water conservation or simply Soil Conservation. The methods of conservation can be broadly put under two groups, *i.e.*, Biological and Mechanical. **The Biological methods** may be (*i*) agronomic (*ii*) agrostological and (*iii*) dry farming. **Mechanical Methods** only aid the Biological ones.

Biological Methods of Soil Conservation

(*a*) **Agronomic Practices**. The science of agronomy has been defined as the theory and practice of crop production in relation to soil. In reality it includes soil conservation and its fertility. The natural growing areas provide a good hint for conservation measures. In a forest we find decomposing plant parts provide organic matter, plants form a useful cover, aeration and drainage of subsurface is improved by root system, soil fertility is maintained by humification and mineralisation. However where a land has been taken up by farmer for its cultivation the problem of conservation arises. If the land is looked after properly it will in turn surely look after the cultivator.

Following agronomic practices will help in conservation :

(*i*) *Contour cultivation*. This is one of the successful methods of checking the effects of run-away water. All agricultural operations up to sowing of seeds are carried along the contour. It reduces the velocity of water, provides it more time for percolation.

(*ii*) *Tillage*. Tilth describes the physical condition of soil that determines its fitness for growing crop. The conditions vary with different types of soils. *Shallow cultivation* avoids weeds and have absorption of more rainfall while *deep cultivation* often leads to soil erosion. On the other hand in Madhya Pradesh 30 cm. deep ploughing with tractors has been found to be effective in weed infested or virgin soil with an annual rainfall of 100 cms. Good tilth and structure facilitate easy and plentiful intake of water, improve aeration, promote easy root growth and activities of microorganisms.

(*iii*) *Artificial Mulching*. Mulch is the protective covering of straw, leaves, twigs, wood chips etc. over the soil. It checks erosion due to wind or water. The water is gradually soaked. The blowing effect of wind is checked. It ultimately adds to the organic matter of soil.

(*iv*) *Crop rotation*. The rotation of crops can be planned de-

pending upon the climatic conditions, type, slope, character, physical and chemical properties of soils. Such crops which check erosion should be sown during the rainy season or when there are wind storms. Legumes find a useful place in rotation of crops because of having nodulated roots which add to the nitrogen content of soil.

(v) *Strip cropping.* It is only another form of crop rotation which covers all the above described methods along with cover cropping. Its different types are :

(a) *Contour strip cropping.* In this the erosion resistant and erosion permitting crops are grown alternately in strips of suitable width. Following table will show the requirements as found by Dry Farming research station, Sholapur.

Slope	Width of Erosion Permitting Crops	Width of Erosion Resisting Crops.
Below 1%	45·72 meters	9·14 meters
1 to 2%	24·40 meters	6·10 meters
2—3%	13·71 meters	4·57 meters

(b) *Wind strip cropping.* This type involves growing alternately tall growing crops and low growing crops at right angle to the direction of winds without taking into consideration the contour.

(c) *Permanent Buffer Strip Cropping.* In this type strips of permanent or temporary nature are planted with perennial grasses, legumes or even shrubs.

(vi) *Cover Cropping.* It is very harmful to keep the soil fallow during rainy season or when strong winds blow. The legumes form a good cover crop during rainy periods. The crops check the erosive effects of water by interception of rain water with their foliage. They check the desiccation of soil due to high temperature in summer.

(vii) *Green manuring.* Basically its practice is meant for increasing soil fertility but it also checks soil erosion. Water holding capacity and drainage conditions are greatly improved which check erosion.

(viii) *Encouraged root growth.* Roots form small channels in the soil while growing downwards or laterally. All the measures undertaken to promote root growth will reduce erosion and help in conservation of soil.

(ix) *Keeping the Soil Surface Rough.* In areas of erosion sohaga should not find any place. The rough surface of soil will have numerous depressions which store water and increase its percolation.

(*x*) *Use of Improved seeds and Fertilisers.* Better the quality of seed more will be its growth. The plant growth and yields depend heavily upon on the quality of seeds and manures added to soil. Thus the adoption of these two practices would mean more yield which in turn will bring higher financial returns. The farmer will thus be able to spare some investment for conservation measures.

(B) Agrostological Methods or role of Grasses in Soil Conservation. Grasses are the pioneers in the ecological cycle. They stabilise soil, conserve moisture, add organic matter by extensive root growth and in turn form a good soil for the growth of better species and other plants. They can easily replace legumes where the latter cannot be cultivated for one or the other reason. Because of their good binding capacity they find a useful place in stabilization of Bunds and Gully Control. Large areas in India have been eroded to such an extent that only 5 to 10 cm. of top soil is left. These areas should be put under grasses after suitably manuring them with nitrogenous and phosphate manures. In America and Britain grasses and agricultural crops are grown in rotation. This is called Lay Farming. It improves the soil structure, prevents erosion, improves fertility of soil and provides good fodder.

Fig. 3·1. Bench Terraces

(C) Dry Farming. This is practised in areas of very low rainfall. Thus the most important factor is to have maximum utilisation and conservation of moisture. The methods are suggested after climatic studies of the area, the soil characteristics, and topography is taken into consideration. Dry farming methods as suggested for Northern India after experimental research are as follows :

(i) Putting 30 cms. high Bunds with bund formers across the slopes.

(ii) Ploughing sandy soils about 12 cms. deep after first rains.

(iii) Growing crops with wider spaces which makes proper utilisation of available water.

(iv) Addition of F.Y.M. annually to keep the fertility of soil.

(v) Keeping the land free of weeds.

(vi) Inclusion of legume in crop rotation. Guar for sandy soils and gram for clay soils is useful.

(vii) Keeping the portion of land fallow for a year or two in rotation.

(D) **Mechanical Methods.** These are devised to supplement the above described measures. The bases for these are (i) to allow more time for absorption of runaway water, (ii) to reduce the velocity of flow and (iii) protect against damages caused by runaway water. The important soil conservation engineering practices are as follows :

(i) *Contour trenches.* Trenches are dug along the contour to trap the silt and intercept water. The sizes of trenches vary according to requirements. This measure increases infiltration, thus keeps perennial flow of water in streams, decreases silt in stream water.

(ii) *Diversion Channels.* Channels are constructed across the slope to check erosive capacity of water and to discharge water at a safe point with non-erosive velocity.

(iii) *Grassed Waterways* and disposal channels are built to receive runaway water and discharge it at a point where no damage of soil takes place.

(iv) *Ponds and tanks* are built to trap silt and runoff water. Water can be used for irrigation purposes. Fisheries can also be made to regulate the supply of water in the rivers and streams.

(v) *Terraces* are made in such a way that the continuity of slope is broken. More time is allowed for percolation of water. There are four types of terraces—Bench terrace, Broad and narrow based ridge terrace and channel terrace.

Bench terraces are costly and are undertaken in areas where land available for cultivation is less. These are cut against the slope with the vertical drop varying from 60 cms. to 120 cms. There are mainly prepared in mountainous and submountain areas. Broad based ridge terraces are prepared in areas of low rainfall and where soil can easily absorb water. The narrow based ridge terraces are

also called bunding. It is the construction of earthen embankments across the slope on the contour., In Punjab Bunds prepared at 0·91 meters vertical interval or 67 meters horizontal distances whichever is less have been successful. Further growing castor on the bunds makes them economically suitable bringing at the same time stability to bunds. These can be built in lands with a slope less than 10%. Channel terraces are prepared in areas of heavy rainfall and where soil is relatively impervious. The wide and shallow channels are made at intervals to intercept water. The soil removed is placed as a low wide ridge along the lower side of channel.

(*vi*) *Gully Control.* The gullies can be controlled and stabilised by having diversion bunds of channels. As far as possible the runaway water should be avoided to form gullies or be minimised in effect. Construction of check dams, overflow dams or spillway are meant for checking advancing gullies. If economically feasible the gullies may be canalised to bring them under vegetation. Growing vegetation holds the .soil permanently. The maximum losses are at the points of curvatures of gullies. They should be smoothened which helps the growth of vegetation and allows smooth flow of water thus reducing erosive effect. Gullies are sometimes stabilised by conversion into rice fields.

(*vii*) *Sub-Soiling.* It involves the breaking of hard impervious lower layers of soil so that they are able to conserve more rain water. The crop yields also increase by deep ploughing. The maximum yields are obtained in Rice in Japan with 35 cm. deep ploughing. The crop yield in Gram was observed to be more than doubled in deep ploughing as compared to the control with undisturbed plot. The implement sub-soiler is coveniently used at a depth of 30 to 60 cms. deep at a spacing of 1 to 2 meters.

(*viii*) *Reservoirs* and *Dams.* Reservoirs are meant to serve the purpose of ponds and tanks at a much bigger scale and to a much bigger extent. They serve as a good source of generation of electric power, regular water supply for irrigation, raising sub-surface water level, and increasing soil moisture. Projects such as Damodar Valley Corporation in Bihar, Bhakra Dam in Punjab and others can be cited as examples of soil and water conservation playing vital roles in economy as well.

Forests & Conservation

Forestry is the foster móther of agriculture. Forests play the

most important role in checking erosion. They may intercept up to 30 per cent of annual rainfall by forming a useful umbrella over the soil. They provide good litter which forms humus providing organic matter to the soil. The porosity and absorption capacity of soil is thus increased for better plant growth. Thick layer of litter of humus underneath a forest may have capacity of infiltration of water from 12 to 15 cms. per hour. This is sufficient even for rainfall of high intensity.

Extensive root growth of forest trees not only provides organic matter to the soil but also binds the soil and increases porosity. They form a good check against wind erosion. Reforestation is the only method of protecting agricultural land against erosion on steep slopes.

Besides these forests provide timber, fuel which can save the ill use of cowdung, their leaves, provide fodder, and manure. They influence to a great deal the local climatic conditions, for example the soil temperature, evaporation from soil and transpiration from plants and thus atmospheric humidity and velocity of wind.

Realising the importance of forests from the national point of view in 1950 Govt. of India and State Govts. started celebrating Van-Mahotsava twice in a year in the months of July and February. According to statistics issued in 1956 only 15% of area of country was under forests, whereas we should have at least 33% for our requirements. In spite of making huge budget provisions in all the Five Year Plans we have not been able to achieve the target. The reason is simple. We plant saplings with great pomp and show but lack of after care results in the death of more than 60% of these seedlings. Planting of trees has been traditional in our country. It had been considered as sacred duty of individuals. *Ficus bengalensis* in East, *Ficus religiosa* in west, *Mangifera indica* in South and *Butea monosperma* towards north be planted while house construction is undertaken by individual has been the sacred order. If we as individuals participate in this project we can add to the national wealth. Along the highway in the villages, plains and hilly areas in the planting of trees every Indian should participate. We can seek the help of forest department which has a network of forest nurseries over the country. The information regarding type of species to be planted the method of plantation, time of plantation and proper care for its growth can be had from the forester. We have the biggest Forest Research Institute in Asia at Dehra Dun. It was established in 1906.

The research covers all the different aspects of forests. Morphology Physiology, Pathology, Entomology, Embryology etc. etc. with respect to forest trees is studied. The various uses to which these can be put to and evolving improved varieties so as to have maximum economic harvest are the other aspects in which useful work has been done and is being done.

Soil Conservation Measures against Wind Erosion

(1) Soil may be kept rough by making furrows at right angle to the direction of wind. Growing crops in furrows is of further aid in checking erosion. Soil cover of vegetation is a useful check against erosion.

(2) Residues of harvested crops should be left on the soil till new crop is to be sown.

(3) Plantation of shrubs and trees be undertaken to provide as wind breaks. These should be 3-4 rows deep. The distance from row to row and plant to plant should vary from 1-3 meters depending upon the heights of the plants grown. First row may be planted with *Zizyphus nummularia*. *Arundo donax*; *Parkinsonia aculeata* or *Prosopis juliflara* plants for 2nd and 3rd row may be *Morus alba*, *Azadirachta indica*, *Acacia nilotica*, or *Acacia modesta* 4th row may be planted of *Eucalyptus*, *Dalbergia sissoo*, *Mangifera indica*, *Eugenia jambolina*

(4) All improved dry farming practices should be adopted.

(5) Trees and grasses should be planted to stabilise the blowing soils.

(6) Make the maximum use of land as it is capable of. It is not necessary that the land must be cultivated for agriculture if the same is not possible. Trees for timber, fodder or fuel may be grown.

Conservation in general may be defined as to avoid the wastage. Minerals, soil, water which are needed by plants and plants and animals needed by man and for his own survival he himself forms the part of environment. In plant ecology conservation of soil and water is mainly dealt with because it is indirectly related to minerals. Nature has certain resources which are not going to be exhausted at all such as atmosphere, water in its saline form, rocks, solar energy. There are other resources which are used up but are renewable such as pure water, soil minerals but not all, CO_2 and O_2 and plants and animals including man. The irreplaceable resources

which are used up in course of time are soils, certain minerls, much of ground water supply, natural landscapes and rare species. Man for his needs has been using the land recklessly with the results that large areas in the world had been made uncultivable. It may be remembered that soil conservation does not mean to take measures at random which only check erosion. It is indeed a well thought out and judiciously planned programme to deal with all aspects of soil and water problems and take all required measures in a determined order.

QUESTIONS

1. What is soil conservation ? Describe various methods of soil conservation adopted in India.

2. Write notes on :
   (*a*) Soil erosion
   (*b*) Forestry
   (*c*) Causes of soil erosion
   (*d*) Effect of soil erosion.

4

TOPOGRAPHIC, GEOGRAPHIC OR PHYSIOGRAPHIC FACTORS

These factors are indirect. They may modify the climatic or edaphic factors. Physiographic factors include behaviour and *structure of earth's surface, altitude, slopes, exposure and direction of the mountains.*

Altitude has modifying effect mainly upon temperature and precipitation components of climatic factors. Light intensity also is affected. In general the greater the altitude the damper the climate. The temperature also decreases as we climb up the mountains. This is due to reduced pressure at higher altitudes. At the sea coast there are sea cliffs composed of different types of rocks. These are constantly being eroded by sea water or rain water forming soil for appearance of plants. The flat coasts, however, have different type of succession. There is silting with salt mud or covering with blown sand where the first colonies appear for succession. Occasionally these colonies may be completely destroyed by tidal or wind erosion for the succession to take place afresh. At the foot of the mountains the vegetation is tropical while at 2000 meters it is temperate gradually changing to Alpine at 3500 meters.

Steepness of slope modifies the water content of soil directly by allowing more of run-away water. The humidity is also affected due to the position of slopes with respect to sun's rays and direction of wind. In the northern areas like ours southern slopes will get sunlight at midday at right angle while northern slopes will get only oblique rays in morning and evening. The effect of wind on the

slopes increases with altitude. The tops of mountains are the worst sufferers due to exposure to strong winds.

The direction and heights of the mountains specially at higher altitudes affect the formation of rains. The frequency of rainfall is more at the tops of mountains because of being enveloped by clouds. The direction of mountains will determine the side which will have more rainfall. The vegetation in turn will thus be more on the side receiving the rainfall than the other.

QUESTIONS

1. Describe Physiographic factors and their effect on vegetation.
2. Describe effect of attitude and slope on the vegetation.

5

ECOSYSTEM

An organism is always in the state of perfect balance with the environment. The environment literally means the surroundings. The environment refers to the things and conditions around the organism which directly or indirectly influence the life and development of the organisms and their populations. Organisms and environment are two non-separable factors. Organisms interact with each other and also with the physical conditions that are present in their habitats. "The organism and the physical features of the habitat form an ecological complex or more briefly an ecosystem." (Clarke 1954).

The concept of ecosystem was first put forth by A. G. Tansley (1935). Ecosystem is the major ecological unit. It has both structure and function. The structure is related to species diversity. The more complex is the structure, the greater is the diversity of the species in the ecosystem. The function of ecosystem is related to the flow of energy and cycling of materisis through structural components of the ecosystem.

According to E. P. Odum, the ecosystem is the basic functional unit of organisms and their environment interacting with each other and with their own components. An ecosystem may be conceived and studied in the habitat of various sizes, *e.g.*, one square metre of grassland, a pool, a large lake, a large tract of forest, balanced aquarium, a certain area of river and ocean. All the ecosystems of the earth are connected to one another, *e.g.*, river ecosystem is connected with the ecosystem of oceans, and a small ecosystem of dead logs in a part of large ecosystem of a forest. A complete self-sufficient

ecosystem is rarely found in nature but situations approaching self-sufficiency may occur.

Componets of ecosystem. According to Odum, all ecosystems; terrestrial or aquatic, from a purely functional or trophic (nutrition) point of view have the following two basic components :

(*i*) *Autotrophic component*, and
(*ii*) *Heterotrophic component*.

The autotrophic component fixes the radiant energy of sun and manufactures food from simple inorganic substances.

The heterotrophic component takes food from autotrophic, rearranges it and finally decomposes the complex organic materials into simple inorganic forms.

In the ecosystems, the autotrophic and heterotrophic components are arranged in layers or strata. The autotrophic metabolism is greatest in the upper stratum where maximum light is available.

In the forest ecosystem, the autotrophic metabolism is maximum in the canopy and in the water ecosystem it is in the surface water where mostly autotrophs are concentrated because of maximum availability of light. The heterotrophic activity is maximum in the lower layer where organic matter accumulates. In the land ecosystems the heterotrophic stratum is the top layer of soil and in aquatic ecosystem it is the bottom sediments.

The ecosystems have structures also and they contain both **non-living** or **abiotic substances** such as water, soil, air and energy and **living** or **biotic components** such as plants, animals and microbes. According to Odum, ecosystems generally include four categories of basic structural components :

(1) Non-living or Abiotic components
(2) Producers, mainly green plants
(3) Consumers, almost exclusively animals.
(4) Decomposers, mainly bacteria and fungi.

Some authors have used a term *reducers* for decomposers. Clarke has recognised *transformers* as the fifth structural component of ecosystems.

Abiotic Components

Ecological relationships are manifested in physico-chemical environment. Abiotic component of ecosystem includes basic inorganic elements and compounds, such as soil, water, calcium, oxygen, carbonates, phosphates and a variety of organic compounds (by-

product of organic activity or death). It also includes such physical factors and gradients as moisture, wind currents and solar radiation. Radiant energy of sun is the only significant energy source for any ecosystem. The amount of non-living components, such as phosphorus, nitrogen etc. that are present at any given time, is known as standing state or standing quantity.

Biotic Components

Producers (Autotrophic elements). The producers are the autotrophic elements—chiefly green plants. They use radiant energy of sun in photosynthetic process whereby carbon dioxide is assimilated and the light energy is converted into chemical energy. The chemical energy is actually locked up in the energy rich carbon compounds. Oxygen is evolved as by-product in the photosynthesis. This is used in respiration by all living things. Algae and other hydrophytes of a pond, grasses of the field, trees of the forests are examples of producers. Chemosynthetic bacteria and carotinoids bearing purple bacteria that also assimilate CO_2 with the energy of sunlight but only in the presence of organic compounds, also come in the category.

The term producer is a misleading one because in an energy context, producers produce carbohydrate and not energy. Since they convert or transduce the radiant energy into chemical form, E. J. Kormondy suggests better alternative terms '*converters*' or '*transducers*'. Because of wide use the term producer is still retained.

Consumers. Those living members of ecosystem which consume the food synthesized by producers are called consumers. Under this category are included all different kinds of animals that are found in an ecosystem. There are different classes or categories of consumers, such as,

(*a*) Consumers of the first order or primary consumers,
(*b*) Consumers of the second order or secondary consumers,
(*c*) Consumers of the third order or tertiary consumers, and
(*d*) Parasites, scavengers and saprobes.

(*a*) *Primary consumers*. These are purely herbivorous animals that are dependent for their food on producers or green plants. Insects, rodents, rabbit, deer, cow, buffalo, goat are some of the common herbivores in the terrestrial ecosystem, and small crustaceans, moluscs etc. in the aquatic habitat. Elton (1939) named herbivores of ecosystem as "Key industry animals". The herbivores serve as the chief food source for carnivores.

(b) *Secondary consumers.* These are carnivores and omnivores. Carnivores are flesh eating animals and the omnivores are the animals that are adapted to consume herbivores as well as plants as their food. Examples of secondary consumers are sparrow, cow, fox, wolves, dogs, cats, snakes etc.

(c) *Tertiary consumers.* These are the top carnivores which prey upon other carnivores. omnivores and herbivores. Lions, tigers, hawk, vulture, etc. are considered as tertiary or top consumers.

(d) Besides different classes of consumers, the parasites, scavengers and saprobes are also included in the consumers. The parasitic plants and animals utilize the living tissues of different plants and animals. The scavengers and saprobes utilize dead remains of animals and plants as their food.

Decomposers and transformers. Decomposers and transformers are the living components of the ecosystem and they are fungi and bacteria. Decomposers attack the dead remains of producers and consumers and degrade the complex organic substances into

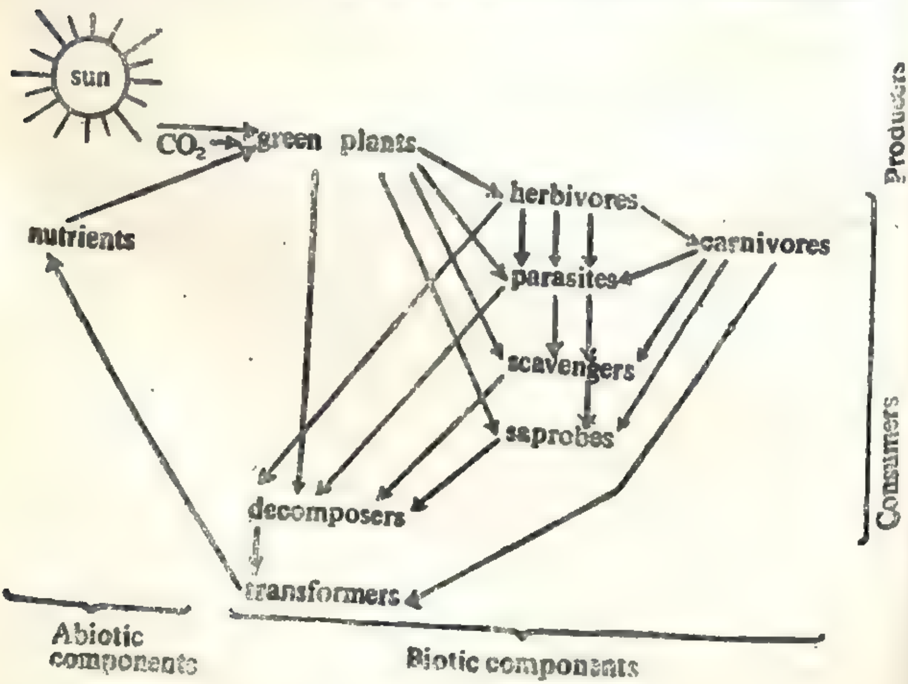


Fig. 5·1. Different components of ecosystem.

simpler compounds. The simple organic matters then are attacked by another kind of bacteria, *transformers* which finally change these organic compounds into the inorganic forms that are suitable for

reuse by producers or green plants. The decomposers and transformers play very important role in maintaining the dynamic nature of ecosystems.

Fundamental steps in the operation of Ecosystem

The principal steps in the operation of ecosystem are as follows :

(1) Reception of radiant energy of sun.

(2) Manufacture of organic materials from inorganic ones by producers.

(3) Consumption of producers by consumers and further elaboration of consumed materials.

(4) After the death of producers and consumers, complex organic compounds are degraded and finally converted by decomposers and converters into such forms as are suitable for reutilization by producers.

The principal steps in the operation of ecosystem not only involve the production, growth and death of living components but also they influence the abiotic aspects of habitat.

It is now clear that there is a transfer of both energy and nutrients from producers to consumers and finally to decomposers and transformer level. In this transfer there is not a progressive decrease of energy but nutrient component is not diminished and it shows cycling from abiotic to biotic and *vice versa.*

The flow of energy is unidirectional. The two ecological processes—energy flow and mineral cycling—which involve inter-action between biotic and abiotic components lie at the heart of ecosystem dynamics. The principal steps and components of ecosystem are illustrated in figure 5·1.

MAJOR ECOSYSTEMS (BIOMES)

According to Whittaker, R. H. (1970), the major type of community, conceived in terms of physiognomy, on a given continent is a *Biome* or *Formation*. 'Biome' is used when the concern is with both plants and animals and formation is used when the concern is with plant communities only. These are the products of inter-action of regional climate with biota and substrate. A biome is a grouping of terrestrial ecosystems on a given continent that are similar in vegetation structure (physiognomy), in the major features of environment to which this structure is a response and in some characteristics of their animal communities. The biome concept which is most widely

applied to land ecosystems can also be applied in aquaitc environment to such zones as the worldwide structural types defined by major kinds of organisms.

In the broadest sense there are two major types of ecosystems namely terrestrial and aquatic.

Terrestrial ecosystem operates on the land while the aquatic system operates in the aquatic habitat (Fig. 5·2).

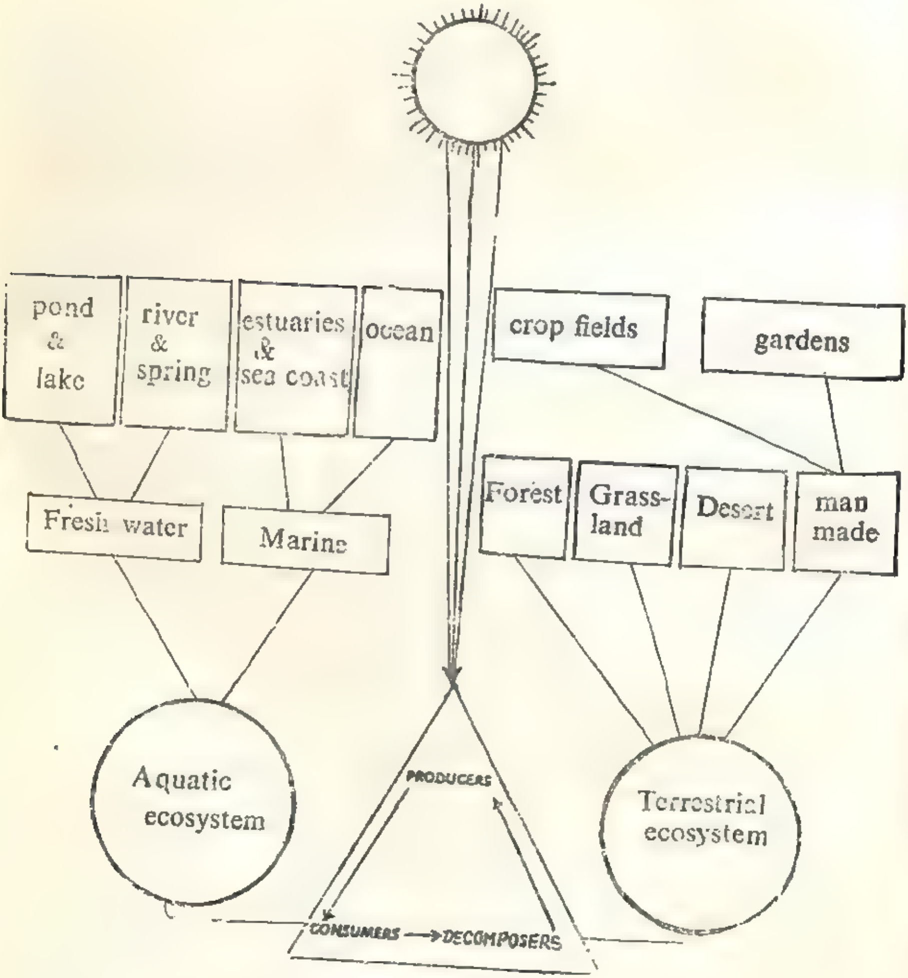


Fig. 5·2. Different types of ecosystem.

Terrestrial ecosystem can further be divided into the following types :

(1) Forest ecosystem
(2) Grassland ecosystem

(3) Desert ecosystem

(4) Artificial ecosystems which are man made, as for example, crop field and gardens.

On the basis of salt contents in water, aquatic ecosystems cau be divided into the following two types of minor ecosystems :

(1) Fresh water ecosystems
(2) Marine or oceanic ecosystems

SOME EXAMPLES OF ECOSYSTEMS

Pond and lake as Ecosystems

Pond is a fresh water ecosystem in which, like other ecosystems, there are two main components :

(A) Abiotic components
(B) Biotic components

(A) Abiotic components. Abiotic component of pond consists of water, dissolved minerals, oxygen and carbon dioxide. Solar radiations are the main source of energy.

(B) Biotic components. It includes the following :

(*i*) Producers
(*ii*) Consumers
(*iii*) Decomposers and transformers.

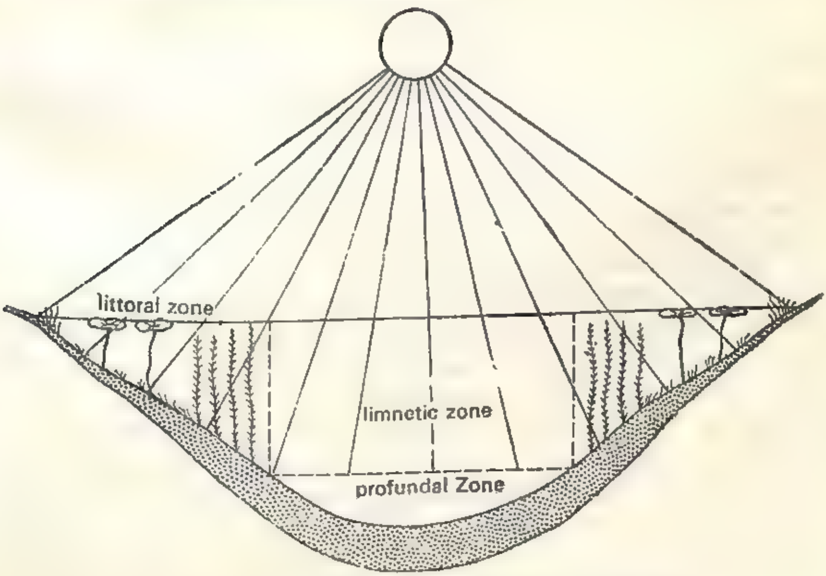


Fig. 5·3a. Different zones of a fresh water pond.

On the basis of water depth and type of vegetation and animals there may be three zones in a lake or pond : *littoral*, *limnetic* and

profundal. The littoral zone is the shallow water region which is usually occupied by rooted plants. The limnetic zone ranges from the shallow to the depth of effective light penetration and associated organisms are small crustaceans, rotifers, insects, and their larvae and algae. The profundal zone is the deep water parts where there is no effective light penetration. The associated organisms are snails, mussels, crabs and worms. (Fig. 5·3*a*)

(i) **Producers**. The main producers in a pond ecosystem are large and other aquatic plants, such as *Azolla, Hydrilla, Potamogeton, Pistia, Wolffia, Lemna, Eichhornia, Nymphaea, Jussiaea* etc. These are either floating or suspended or rooted at the bottom. The green plants convert the radiant energy into chemical energy through photosynthesis. The chemical energy stored in the form of food is utilised by all the organisms. Oxygen evolved by producers in photosynthesis is utilised by all the living organisms in respiration.

(ii) **Consumers**. In a pond ecosystem, the primary consumers are tadpole larvae of frogs, fishes and other aquatic animals which consume green plants and algae as their food. These herbivorous aquatic animals are the food of secondary consumers. Frogs, big fishes, water snakes, crabs are secondary consumers. In the pond, besides the second consumers, there are consumers of highest order, such as water birds, turtles, etc.

(iii) **Decomposers and Transformers**. When aquatic plants and animals die a large number of bacteria and fungi attack their dead bodies and convert the complex organic substances into simpler inorganic compounds and elements. These micro-organisms are called *decomposers*. The chemical elements liberated by decomposers are again utilized by green plants in their nutrition (Fig. 5·3*b*).

Ocean as an ecosystem

The oceans constitute nearly 70 per cent of the earth's surface. The sea has unusual stability in temperature, salinity and gaseous content. The upper portion of the oceanic region through which light penetrates is called euphotic zone. The region of the ocean below the euphotic zone (below 200 metres) is called *benthal*. It is also known as aphotic zone. This zone is completely free of photosynthetic organisms. Thus, a different set of environment and conditions is present in each one of the ocean zones and each zone has its own peculiar life form. Planktonic organisms are algae, diatoms, protozoans, small crustaceans and their eggs. The seashore organisms live under variable physical conditions and they are constantly under the impact of waves. Most of them are covered and exposed twice daily by the rise and fall of the tides.

Streams and Rivers

In the rivers and streams in the shallow water the velocity of current is great to keep the bottom clear. Filamentous algae and fishes are common examples. In the zone of deep water the velocity of water current is reduced and silt and other loose materials tend to settle at the bottom.

Wet Lands

These are marshes and swamps which are low lying wet lands and their ecosystem is suitable for ducks and other semi-aquatic animals. Swamps also support large trees and shrubs. They have various types of environmental conditions, both aquatic and semi-aquatic. Aquatic insects, reptiles and birds are common in such regions.

Forest as an Ecosystem

Forest ecosystem is the best example of a terrestrial ecosystem. Like other ecosystèms, there are two main components of forest ecosystem :

(A) Abiotic component

(B) Biotic component.

(A) Abiotic component. In a forest ecosystem soil, moisture, air and sunlight form the abiotic or physical component.

(B) Biotic component. There are three important classes of biotic components :

1. Producers
2. Consumers
3. Decomposers and transformers.

1. Producers.. All the green plants of a forest are producers. They are the main sources of food for all the animals. There are several layers of vegetation in the forest. The plants of top stratum are angiospermous and gymnospermous trees. These plants utilize radiant energy of sun to a greatest extent. Below the level of trees there is layer of shrubs which consume light energy of low intensity coming through trees. Just below the shrubs there are grasses, herbs, lichens and mosses. These also manufacture food. These plants get least light.

2. Consumers. There are a number of consumers in an old dense forest. Consumers of first order in the forest are grasshoppers, rabbit, deer, monkey, birds and many other wild herbivorous animals

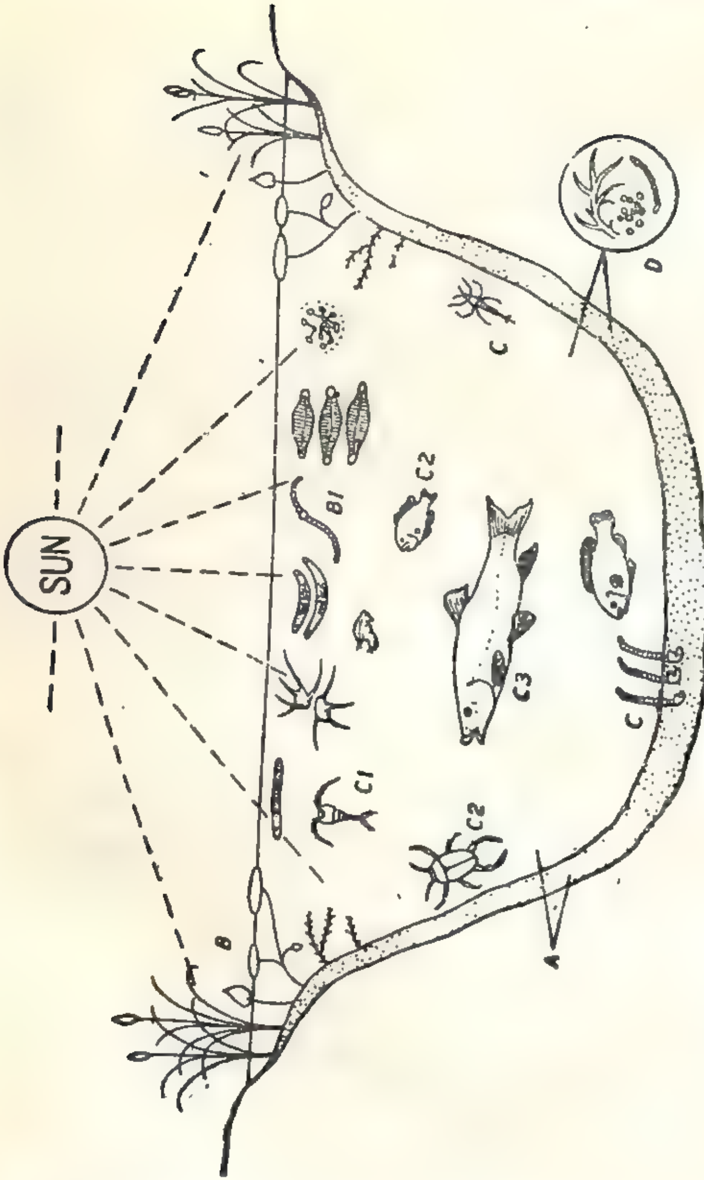


Fig. 5·3b—A pond ecosystem.

A—Abiotic component ; B and B1—Producers ; C1—Primary consumers (herbivores) ; C2—Secondary consumers ; C3—Tertiary consumers ; D—Decomposers—saprophytic bacteria and fungi.

which utilize plants directly as their food. Secondary consumers are wolves, pythons, jackals etc. which consume the flesh of herbivores. Lion, tiger, hawks are the consumers of top level.

3. **Decomposers and transformers**. These are micro-organisms, chiefly bacteria and fungi which attack dead bodies of producers and consumers and convert complex organic compounds into simpler inorganic compounds and elements. These free elements

again return to the abiotic component and are re-utilised by producers in their nutrtiion.

Artificial Ecosystems

Gardens, parks, vegetable gardens and agricultural lands are the artificial or man-made ecosystems. A balanced aquarium is also an artificial ecosystem. The space capsule which lasts for limited period is also an artificial ecosystem. For longer journey on space-craft includes all the basic components of the ecosystem, namely producers, consumers, decomposers and abiotic components.

Ecological Niches. Species of plants and animals present in an ecosystem perform different functions. Role of each species is spoken of as its niche. In other words, the total role of a species in the community is the ecological niche. The ecological niche includes the species of organisms, environmental factors, the area in which the species live and the specialization of species population within a community. Every population has an ecological niche, which determines the structure and adaptation of that population. Ecological niche is not a simple concept but it relates the concepts of population and community. The niche is the property of the community which represents the place of the population in the community structure. Different communities in ecosystem characterised by similar environments are often similar in their structure and they may contain one or more niches that are essentially identical. The adaptations of population inhabiting these niches may also be similar, even though they are entirely unrelated.

Nature of energy

Energy has been defined as the capacity to do work. It exists in various forms. The forms of energy that are of the greatest sigcnificance to the living organisms are mechanical, chemical, radiant and heat energy.

The source of energy required by all living organisms is the chemical energy of their food. The chemical energy is obtained by the conversion of the radiant energy of sun. The radiant energy is in the form of electromagnetic waves which are released from the sun during the transmutation of hydrogen to helium. The chemical energy stored in the food of living organisms is converted into potential energy by the arrangement of the constituent atoms of food in a particular manner.

Mechanical energy exists in two forms : potential and kinetic. Potential energy is the energy at rest (*i.e.*, stored energy) capable of

performing work. Kinetic energy is the energy of motion (free energy). It results in work performance at the expense of potential energy. Conversion of potential energy into kinetic energy involves the imparting of motion. In any ecosystem there should be uni-directional flow of energy. This energy flow is based on two important laws of thermodynamics which are as follows :

(1) **The first law of thermodynamics**- It states that the amount of energy in the universe is constant. It may change from one form to another, but it can neither be created nor destroyed. Light energy can be neither created nor destroyed as it passes through the atmosphere. It may, however, be transferred into another type of energy, such as chemical energy or heat energy. These forms of energy can be transformed into electromagnetic radiation.

(2) **The second law of thermodynamics**. It states that non-random energy (mechanical, chemical, radiant energy) cannot be changed without some degradation into heat energy. The change of energy from one form to another takes place in such a way that a part of energy assumes waste form (heat energy). In this way, after transformation the capacity of energy to perform work is decreased. Thus, energy flows from higher to lower level.

Main sources of energy is sun. Approximately 57% of sun energy is absorbed in the atmosphere and scattered in the space. Some 35% is expanded to heat water and land areas and to evaporate water. Of the approximately 8% of light energy striking plant surface, 10% to 15% is reflected, 5% is transmitted and 80 to 85% is absorbed; and an average of only 2% (0.5 to 3.5%) of the total light energy striking on a leaf is used in photosynthesis and rest is transformed into heat energy.

Energy flow in ecosystems. Living organisms can use energy in several forms: *radiant* and *fixed energy*. Radiant energy is in the form of electromagnetic waves, such as light. Fixed energy is potential chemical energy bound in various organic substances which can be broken down in order to release their energy content.

Organisms that can fix energy from inorganic sources into organic molecules are called autotrophs. Organisms that cannot obtain energy from abiotic source but depend on energy-rich organic molecules synthesised by autotrophs are called heterotroph. Those that obtain energy from living organisms are called consumers and those that obtain energy from dead organisms are called decomposers.

When the light energy falls on the green surfaces of plants, a

part of it is transformed into chemical energy which is stored in various organic products in the plants. When the herbivores consume plants as food and convert chemical energy accumulated in plant products into kinetic energy, degradation of energy will occur through its conversion into heat. When herbivores are consumed by carnivores of the first order (secondary consumers), further degradation will occur. Similarly, when primary carnivores are consumed by top carnivores, again energy will be degraded.

Trophic level. The producers and consumers in ecosystem can be arranged into several feeding groups, each known as *trophic level* (feeding level). In an ecosystem, producers represent the first trophic level, herbivores represent the second trophic level, primary carnivores represent the third trophic level and top carnivores represent the last level.

Food Chain

In the ecosystem, green plants alone are able to trap in solar energy and convert it into chemical energy. The chemical energy is locked up in the various organic compounds, such as carbohydrates, fats and proteins in the green plants. Since virtually all other living organisms depend upon green plants for their energy, the efficiency of plants on any given area in capturing solar energy sets the upper limit to long-term energy flow and biological activity in the community. The food manufactured by the green plants is utilized by themselves and also by herbivores. Animals feed repeatedly. Herbivores fall prey to some other carnivorous animals. In this way one form supports the other form of life. Thus, food from one trophic level reaches to the other trophic level and in this way a chain is established. This is known as *food chain.* A food chain may be defined as the transfer of energy and nutrients through a succession of organisms through repeated process of eating and being eaten. In food chain initial link is a green plant or producer which produces chemical energy available to consumers. For example, marsh grass is consumed by grasshopper, the grasshopper is consumed by a bird and that bird is consumed by hawk. Thus, a food chain is formed which can be written as follows:

$$\text{Marsh grass} \rightarrow \text{grasshopper} \rightarrow \text{bird} \rightarrow \text{hawk}$$

Food chain in any ecosystem runs directly in which green plants are eaten by herbivores, herbivores are eaten by carnivores and carnivores are eaten by top carnivores. Man forms the terrestrial link of many food chains.

Food chains are of three types :

1. **Predator Chain**. Which starts from plant and goes from smaller to larger animals.

2. **Parasitic Chain**. It goes from large to smaller organisms.

3. **Saprophytic Chain**. It goes from dead matter to micro-organisms. It is also known as *detritus food chain*.

The energy contained in this detritus is not lost to the ecosystems as a whole, but it serves as the source of energy for a group of organisms which is called detritus food chain.

Food Web. Many food chains exist in an ecosystem, but as a matter of fact these food chains are not independent. In ecosystem, one organism does not depend wholly on another. The resources are eaten by variety of insects, birds, mammals and fishes and some of the animals are eaten by several predators. Similarly, in the food chain, grass→mouse→snakes→owls, sometimes mice are not eaten by snakes but directly by owls. This type of interrelationship interlinks the individuals of the whole community. In this way, food

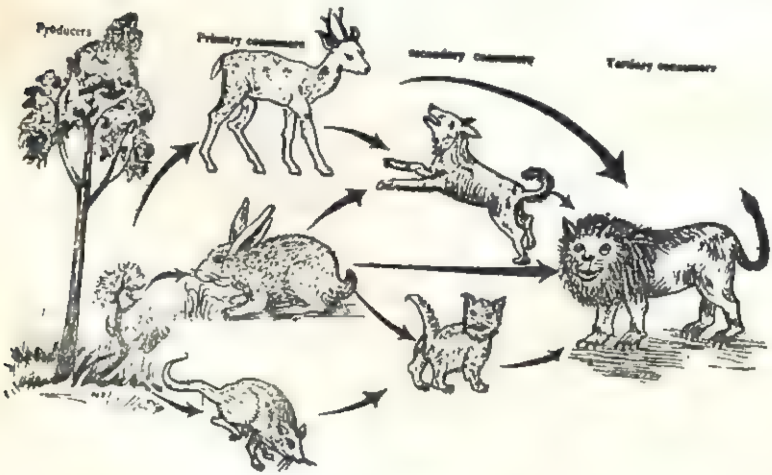


Fig. 5.3c—Food web in an ecosystem.

chains become interlinked. A complex of interrelated food chains makes up a food web. Food web maintains the stability of the ecosystem. The greater the number of alternative pathways the more stable is the community of living things. Fig. 5.3c illustrates a food web in ecosystem.

Ecological pyramid. At each step in the food chain a considerable portion of the potential energy is lost as heat. As a result, organisms in each trophic level pass on lesser energy to the next trophic level than they actually received. This limits the number of steps in any food chain to 4 or 5. Longer the food chain the lesser energy is available for final members. Because of this tapering off of available energy in the food chain a pyramid is formed that is known as ecological pyramid. The higher the step in the ecological pyramid the lower the number of individuals and the larger their size.

The use of ecological pyramids was advanced by C.E. Elton (1927). There are different types of ecological pyramids. In each ecological pyramid producer level forms the base and successive levels make up the apex. These types of pyramidal relations may be found among the organisms at different levels in the ecosystem.

Productivity

Green plants fix solar energy and accumulate it in the organic material in chemical form. The energy accumulated by producers is called *production* or more especially *primary production*. Since it is the first and basic form of energy storage, the rate at which the energy accumulates in the green plants or producers is known as **primary productivity.** Primary productivity is the rate at which energy is bound or organic material is created by photosynthesis per unit of earth's surface per unit time ; it is most often expressed as energy in calories $/ cm^2 / yr$ or dry organic matter in $g / m^2 / yr$ ($gm^2 \times 8.92 = lb. / \text{acre}$). The amount of organic matter present at a given time per unit area is called **standing crop** or **biomass** and as such productivity, which is a rate, is quite different from biomass or standing crop. The standing crop is usually expressed as dry wt. g/m^2 or kg/m^2 or as t/ha (metric tons), $10^6 g$/hectare. Primary productivity is the result of photosynthesis by green plants including algae of different colours. Bacterial photosysthesis or chemosynthesis although of small significance may also contribute to primary productivity. The total solar energy trapped in the food material by photosynthesis is referred to as **gross primary production**.

A good fraction of gross primary production is utilized in respiration of green plants. The amount of energy-bound organic matter created per unit area and time that is left after respiration of these plants is **net primary production** or **Plant growth**. Only the net primary productivity is available for harvest by man and other animals. Net productivity of energy = gross productivity − energy

used in respiration. The rates at which the heterotrophic organisms resynthesize the energy yielding substances is termed as *secondary productivities*. Secondary productivities are the productivities of animals and saprobes in communities.

There are three fundamental concepts of productivity :

1. Standing crop
2. Materials removed
3. Production rate.

1. Standing crop. It is the abundance of the organisms existing in the area at any one time. It may be expressed in terms of number of individuals, as biomass of organisms, as energy content or in some other suitable terms. Measurement of standing crop reveals the concentration of individuals in the various populations of the ecosystem.

2. The materiais removed. The second concept of productivity is **the materials removed** from the area per unit time. It includes the yield to man, organisms removed from the ecosystem by migration, and the material withdrawn as organic deposit.

3. The production rate. The third concept of productivity is the **production rate**. It is the rate at which the growth processes are going forward within the area. The amount of material formed by each link in the food chain per unit of time per unit area or volume is the production rate.

All the three major groups of organisms – producers, consumers and reducers are the functional kingdoms of natural communities. The three represent major directions of evolution and are characterised by different modes of nutrition. Plants feed primarily by photosynthesis-animals feed primarily by ingesting food that is digested in and absorbed from an internal cavity and the saprobes feed by absorption and have need for an extensive surface of absorption. The principal kinds of organization evolved among saprobes are the unicellular bacteria, yeasts, chytrids of lower fungi and a higher fungi with mycelial bodies.

In terrestrial communities as much as 90% of net primary production remains unharvested and must be utilized as dead tissue by saprobes and soil animals. In terrestrial ecosystems, the saprobes have a larger and more essential role than animals in degrading dead organic matter to inorganic forms and in such ecosystems, secondary production by reducers (decomposers) should exceed that by consumers, though the former is even more difficult to measure than the latter. Biomass of decomposers with their microscopic cells and

filaments embedded in good sources, is also difficult to measure and that is small in relation to their productivity and significance for the ecosystem. Small masses of reducers degrade and transform for larger masses of organic matter to inorganic remnants. In so doing decomposers disperse back to the environment the energy of photosynthesis accumulated in the organic compounds that decompose. Thus, they have a major part in the energy flow of ecosystems. A community or ecosystem, like an organism, is an open energy system. The continuous intake of energy by photosynthesis replaces the energy dissipated to environment by respiration and biological activity and the system does not run-down, through the loss of free energy to maximum entropy. If the amount of energy entrapped is greater than the energy dissipated, the pool of biologically useful enegy of organic bonds increases. This results in increase of community biomass and consequently the community grows ; such is the case in succession. If energy intake is less than energy dissipation, the community biomass will decrease and it must, in some sense, retrogress. If energy intake and loss are in balance, the pool of organic energy is in steady state; such is the case in climax communities. Three aspects of this steady state may be recognised : (*i*) The steady state of populations of climax communities in which equal birth and death rates in population keep the number of individuals relatively constant, (*ii*) The steady state of energy flow, (*iii*) The steady state of the matter of community, where addition of material by photosynthesis and organic synthesis is balanced by loss of material respiration and decomposition.

BIOGEOCHEMICAL CYCLES

Nearly 30 to 40 elements are required for the proper growth and development of living organisms. Most important of these are C, H, O, P, K, N, S, Ca, Fe, Mg, B, Zn, Cl, Mo, Co, I and F. These materials flow from abiotic to biotic components and back to the non-living component again in a more or less cyclic manner. This is known as the biogeochemical cycle or inorganic-organic cycle. The flow of these elements through the ecosystem must be cyclic, with matter being consistently reused. Because the flow involves not only living organisms, but also a series of chemical reactions in the abiotic environments, these cycles are called biogeochemical cycles.

There are three type of biogeochemical cycles.

(1) Hydrologic cycle or water cycle,

(2) Gaseous cycle,

(3) Sedimentary cycle.

1. Hydrologic or water cycle. Interchange of water between atmosphere, land and sea and between living organisms and their environment is accomplished through water cycle. Water cycle or hydrologic cycle involves evaporation, transpiration, cloud formation, precipitation, surface water run off and percolation. Of these, the key process is evaporation since it maintains the humidity of the atmosphere and feeds back the moisture necessary for cloud formation and precipitation. Water of atmosphere reaches to the earth surface through precipitation and from the earth surface it reaches to the atmosphere through evaporation and transpiration. The amount of water available for evaporation is determined by the amount supplied by precipitation and condensation. Between rainfall input and evaporation output there lies a precarious water balance (Fig. 5.4).

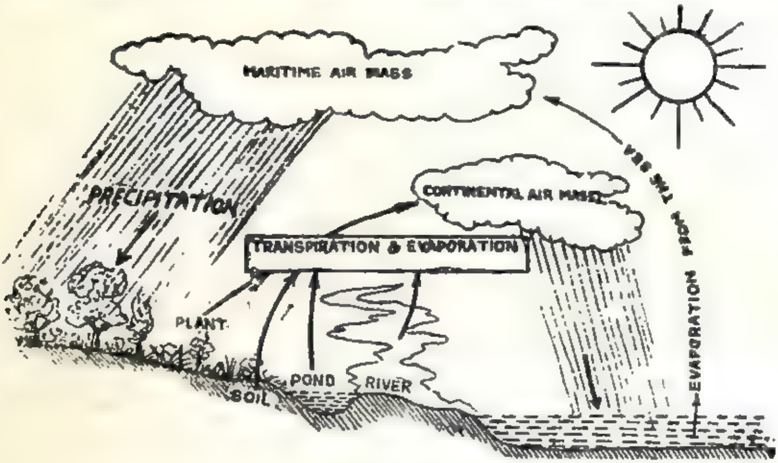


Fig. 5.4-Hydrologic cycle in nature.

3. Gaseous Cycle

Oxygen cycle. Oxygen is found in free state in atmosphere and in dissolved state in water. It is liberated as byproduct of photosynthesis and is utilized in respiration by all the plants and animals. When the living organisms respire, CO_2 is liberated which is utilized by green plants as an essential raw material for carbohydrates synthesis. In this way a simple yet vital O_2 cycle is maintained in the ecosystem.

Carbon cycle. Carbon is the basic constituent of all organic compounds. Since energy transfer occurs in the consumption and storage of carbohydrate and fats, carbon moves to the ecosystem with flow of energy. The source of nearly all carbon found in the

living organisms is CO_2 which is found in free state in atmosphere and in dissolved state in the water on the earth. Green plants (producers) use CO_2 through photosynthesis in the presence of sunlight and carbohydrate is formed. Later on complex fats and polysaccharides are formed in plants which are utilized by animals. Flesh eating animals (carnivores) feed on herbivores and the carbon compounds are again digested and converted into the other forms. Carbon is released to the atmosphere directly as CO_2 in respiration of both plants and animals. Bactaria and fungi attack the dead remains of plants and animals. They degrade the complex organic

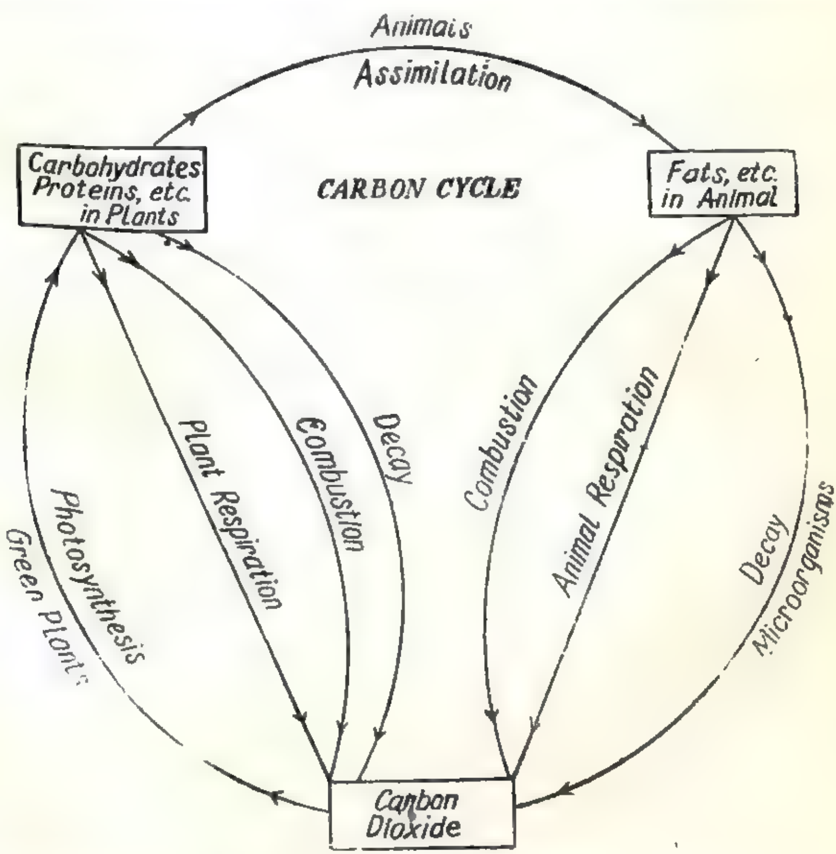


Fig. 5.5.—Carbon cycle in ecosystem

compounds into simple substances, which are then available for other cycles. Part of the organic carbon becomes incorporated into the earth's crust as coal, gas, petroleum, limestone and coral reef. Carbon from such deposits may be liberated after a long period of time (Fig. 5.5).

Nitrogen cycle. Of all the elements which plants absorb from the soil nitrogen is most important for plant growth. This is required in greatest quantity. Green plants obtain nitrogen from the soil solution in the form of ammonium or nitrates or nitrite ions. The most important source of nitrogen for green plants is nitrogen that is fixed by nitrogen fixing bacteria. Some of the nitrogen fixing bacteria inhabit the root nodules of leguminous and some other plants and some others are free in the soil. Nitrogen is directly taken from the air by nitrogen fixing root nodule bacteria (rhizobia) or by free living aerobic bacteria (*Azotobacter*) or by anaerobic soil bacteria (*Clostridium*). These bacteria make nitrogen available to the plants and add to their growth. Some blue green algae, as for example, species of *Nostoc* and *Anabaena* also perform nitrogen fixation. When nitrogen is absorbed as nitrate it has to be reduced to ammonia before being used in amino acid and protein synthesis. The

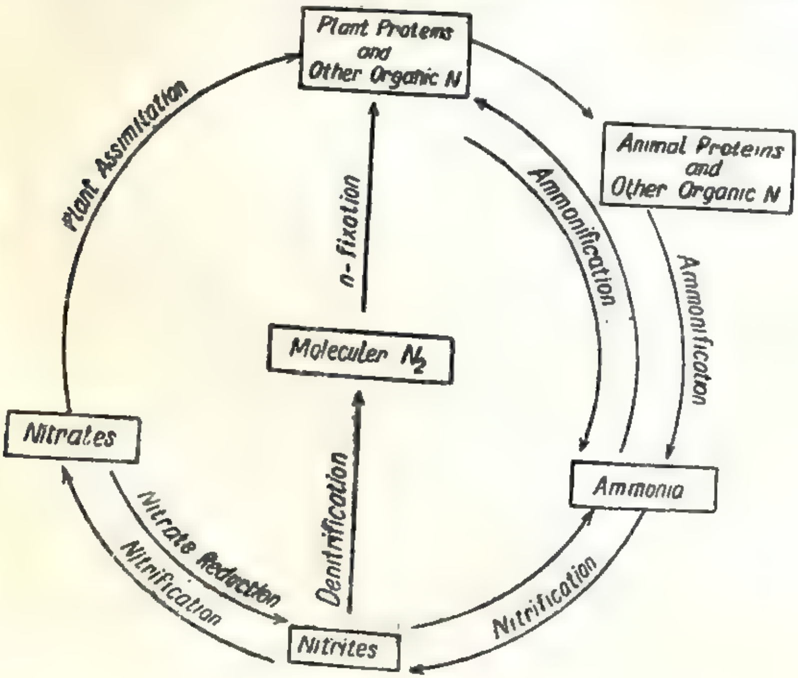


Fig. 5.6.—The nitrogen cycle in ecosystem

breakdown of dead tissues by decay bacteria releases ammonia from protein and other nitrogenous compounds. Nitrosomonas bacteria oxidize ammonia into nitrites and still other bacteria (Nitrobacter) oxidize nitrite to nitrate (Nitrification). Ammonia is also directly converted into free nitrogen by denitrifying bacteria (Denitrification). In this way, the nitrogen cycle is repeated in the ecosystem.

The overall nitrogen cycle in nature is represented in Fig. 5.6.

3. Sedimentary Cycle

Mineral elemenrs required by living organisms are obtained initially from inorganic sources. Available forms occur as salts dissolved in soil water. Mineral cycle essentially consists of two phases : (*i*) The salt solution phase and (*ii*) rock solution phase.

Mineral salts come directly from earth crust by weathering. Soluble salts then enter the water cycle. By movement of water minerals move from the soil to streams, lakes and ultimately to sea where they remain permanently. Other salts return to the earth's crust through sedimentation. They become incorporated into sediments or beds and after weathering of rocks they again enter the cycle. Plants and some animals take minerals in the form of mineral solution from their habitats. After the death of living organisms the minerals return to the soil and water through the action of decomposers (bacteria and fungi) and transformers. Green plants at one end and decomposers at another play very important role in circulation of nutrients.

Phosphorus cycle. Plants and animals obtain phosphorus from the environment and when they die the decomposers attack them and liberate phosphorus to the environment. This process proceeds in cyclic way. Phosphorus, calcium and many other elements also reach the oceans in dissolved state and there they undergo sedimentation (accumulation). In the sedimentary deposits the nutrients are locked up for indefinite period and in this way, they are separated from the cyclic pathway. When sediments weather, the nutrients become free for another cycle.

Other Nutrient cycles

The nutrient cycle is not a close circuit within an ecosystem. The nutrients are continuously being imported as well as being carried out of the ecosystem. Appreciable quantities of plant nutrients are brought to ecosystem by rain and snow. Small quantity of nutrients carried to the forest is by rains. The gain of nutrients to the ecosystem from precipitation, extraneous material and mineral weathering is offset by losses. Water draining away from forest carries with it more mineral matter than supplied through precipitation. Considerable quantities of nutrients in the forest are locked up in the trees and the humus layer. When trees and vegetation are removed, sufficient amount of nutrient is removed. Intensive forestry and agriculture on some soils may reduce the

nutrient reserves to such an extent that soils become unfertile. Ecosystem can remain productive only if the nutrients withdrawn are balanced by an inflow or replacement.

QUESTIONS

1. What is ecosystem ? What are the various components of ecosystem ?
2. What are the major ecosystems of the world ? Describe forest and pond ecosystems in detail.
3. What is meant by energy flow in an ecosystem ? What are the laws of thermodynamics ?
4. Write short notes on the following :

   Producers, Food chain and Food web, Ecological pyramid, Hydrologic cycle, Nitrogen cycle, Productivity.

6

PLANT COMMUNITIES

Synecelogy is the branch of ecology which deals with the study of interrelationship of environment and community. There are unicellular organisms which have all physiological functions being performed by a single cell. These in evolutionary sequence have formed multicellular organisms with physiological division of labour. These organisms do not live in isolation but are found in nature as groups of individuals. The groups of individuals living in a particular area constitute community. In the community we may find both plants and animals living together. In the present text we will study only Plant community. Plant community as a whole can be given an individual entity. Like unicellular plant or multicellular plant it has its birth, growth and maturity. Wherefrom the community comes ? Just as a unicellular or multicellular organism has its origin from reproductive bodies, community also arises from the spores or seeds of preexisting communities. The development of plant community consitutes a **succession**. It involves stages of migration ecesis (the establisment in a new home involving germination, growth and reproduction), Competition, Reaction and formation of climax community. Like a tree which has root, stem and its branches, leaves, flowers etc. a plant community also has its various components. Its components are *formations, associations, consociations societies, colonies, families and species.* **Plant formations** are the communities produced under similar climatic conditions. It is the main unit of vegetation. The major classes of formation recognised are Evergreen forests, Rain forests, Coniferous forests, Deciduous forests, Evergreen or deciduous or dwarf Scrubs, Savanna, Grassland, Meadows, Wood land or Steppe forest, Desert forest, scrub or

herb etc. In the formation we find that there are certain species which control the environment or climate of that area, these are called as **dominants**. In a particular localised area, there may be a single such species or more than one species may be exerting the controlling influence. It is the dominants which determine the occurrence and distribution of other plants within the formation.

The Association. The plant formation is made up of plant associations. It is the unit of vegetation represented by uniform physiognomy, ecological structure and floristic composition. Physiognomy means the external form, ecological structure includes the behaviour of plants to the environmental factors and floristic composition refers to the species of plants. While in the expression of first and third aspect mainly dominants are considered the second aspect takes into consideration the secondary plants as well. Thus an Association may be denoted as Evergreen forest (Physiognomy), mesic (Ecological structure), Cedrela Dipterocarpus association (Floristic composition).

The Consociation. It is an association in which there is a single dominant species or that part of an association which is represented by a single dominant species. In case an association has only single dominant species it is consociation but normally an association has several dominants, thus there will be as many consociations as dominants in an association.

Faciations. Since association may have several dominants there will be certain areas in which dominants may be more than one. Such portions of the associations which are occupied by more than one dominants and less than the total number in an association are called Faciations.

Society. In an association there are not only dominant species but also the sub-dominants. These sub-dominants control the appearance instead of environment which the dominants control. The sub-dominants constitute that morphological part of association which is called a society. In general three kinds of societies are recognised. *Aspect societies* are the commonest which consist of herbs becoming conspicuous in appearance when flower. *Layer societies* constitute the layers such as shrub layer, herb layer or cryptogamic layer. *Cryptogamic societies* are represented by mosses, hepatics, fungi and lichens.

Colony represents the group of plants which invade a bare area. When these plants hail from a single ancestral plant they are referred to as **family**. However, it is better to use the word colony

even for plants from single species because family in taxonomy is used in a quite different sense.

Seral communities. All the above described terms such as association, consociation, faciation and society are used for mature climax communities. However, we may find communities yet in the process of development heading towards maturity, for such seral communities the terms used are *associes*, *consocies*, *facies* and *socies* respectively.

Plant Succession

We have already observed that plant community like individual organism has its life history. This universal process of development of community is called **succession**. The various stages observed in its development constitute **seres**. The succession always starts its growth on a bare area. Such bare areas may be primary or secondary. The *primary area* is one which had no plant life before in any form. It may be sand, rock or water. Primary bare areas may appear due to volcanic eruptions, appearance of islands due to elevation, erosion due to elevation, erosion due to wind, water and gravity. *Secondary bare areas* are those which had plant life but were destroyed completely by one or the other factor. They may be produced due to the action of climatic factor such as severe frost may kill the plants completely; biotic factors such as man may destroy the vegetation completely to make the areas bare. In secondary bare areas there is natural presence of some organic matter in decomposed or undecomposed form left as such. Spore or seeds or other organs of vegetative propagation may also escape destruction. Succession may start on water or wetter areas or on rock or drier areas. The seres are correspondingly defined as :

Priseres	when succession appears			on primary bare area
Subseres	„	„	„	secondary bare area
Hydrosere	„	„	starts	in fresh water
Halosere	„	„	„	in saline water
Xerosere	„	„	„	in dry area
Psammosere	„	„	„	in sand
Lithosere	„	„	„	in rock

Hydrarch is the term used when successional series proceed from Hydric to mesic.

Xerarch is the term used when successional series proceed from xeric to mesic.

In Hydrarch the primary or secondary bare area is either water or a wetter area than the climax while in Xerarch the area is either

a sand or rock drier than the climax. Thus we find that whether succession starts in water or on rock it generally tends to become mesic ultimately. The general stages in succession are :

(*a*) Migration
(*b*) Ecesis
(*c*) Competition
(*d*) Reaction
(*e*) Maturity or Climax.

(*a*) **Migration**. All plants possess the effective organs of reproduction which are shed and dispersed. These may be the spores of various forms in lower non-vascular or vascular plants or seeds and other organs of vegetative reproduction in seed bearing plants. The fruits as such in indehiscent types or seeds in dehiscent types are adapted to the effective dispersal. The agencies which bring about dispersal are wind, water, animals including man and explosive mechanism. The various adaptations for wind dispersal are, light and small seeds in orchids, hairy pappus, in composites, hairy outgrowth in calotropis, winged outgrowth in Pinus, Elm. Water brings about effective dispersal mainly of hydrophytes or plants growing on the banks of water. The effective distance to which these can be carried depends upon permeability to water. Animals bring about dispersal either by eating fruits, having indigestible seeds or by attachment to their bodies. The latter may have sticky pulp or spines or hook-like outgrowths. Many animals store fruits and seeds as their food and then forget about their recovery or are forced to leave the places of storage due to conditions beyond their control. Migration brings about the birth of a community on a bare area. It leads to ecesis.

(*b*) **Ecesis**. It involves germination, growth and reproduction which results only if the organs of migration get themselves settled in the new homes. Germination of fruits and seeds in majority of plants except viviporous requires the breaking up of Dormancy. Dormancy period varies from plant to plant so also the cause of dormancy such as immature embryo, hard seed coat, gaseous or enzyme requirements etc. The germination ultimately leads to the formation of seedlings. The mortality at this stage of community development is often very high. They survive only under favourable environmental conditions. If the seedlings are able to survive further growth proceeds to maturity depending upon the various ecological factors. The vegetative growth is followed by reproductive growth The reproductive organs may be vegetative such as rhizomes, corm,

bulb though effective means of propagation are very slow invading or they may be fruit and seeds which complete ecesis.

(*c*) **Competiton**. Since different species migrate simultaneously the bare areas, this leads to competition between some. The species which have similar requirements of nutrition are known as competitive species while there are others which can live in community without competition are called complimentary species. To begin with roots compete in soil for moisture and nutrients and this is followed by shoot competition mainly for light. It may be inter or intraspecific, inter or intrageneric. Only such species succeed in competition who have some advantages over others.

(*d*) **Reaction**. It is not the environment which only affects plants. Plants also produce their effect on the environment which is called reaction. The first effects are on the substratum. They lead to the formation of soil from rocks, add material to soil. They change the structure and texture of soil in course of time by addition of humus. The soil water and air composition is also affected. As we shall see in the discussion on two examples of succession to follow that in the Hydrosere water becomes less as succession proceeds towards maturity while in Xerosere water becomes more above soil. In atmosphere the effect is of cutting light, increasing humidity, decreasing temperature and velocity of wind.

(*e*) **Climax Community**. The reactions of individuals collectively have a wider effect on the environment. The local climate is actually changed if the climax vegetation is forest. The reactions keep the vegetation in active state till the climax community is formed. Although strictly speaking vegetation can never be called as stable yet at maturity the community being mesic further mesic changes being less possible the climax community can be called as relatively stable. Thus ultimately we find the development of community living in harmony within the environment which has been the result of its reactions.

Successions according to reacation are called **autogenic** or **allogenic**. In the former the rection of the plants themselves and in the latter reaction of the climatic or topographic factors play an important role. Strictly speaking succession is never entirely autogenic or allogenic.

HYDROSERE

As already defined hydrosere represents the succession on fresh water. It may take place in flowing water or standing water. The

one around the standing water can be best studied because of zonation of various stages in its development. The stages are :

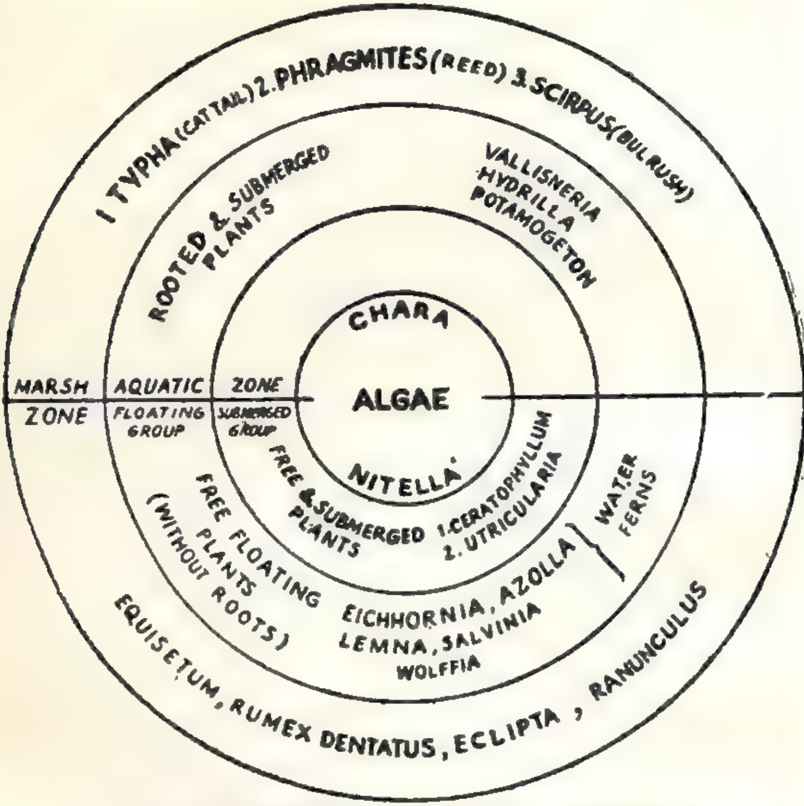


Fig. 6·1. Vegetation in and around a water reservoir

(1) Submerge Stages. First plants which appear are submerged aquatics. These may be algae or flowing plants like

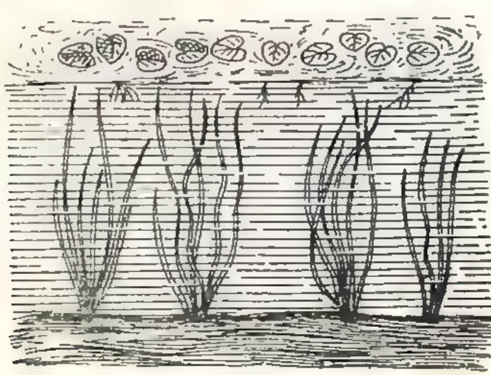


Fig. 6·2. Submerged stage

Lemna, Potamogeton, Hydrilla. The depth of water is about 3-4

metres. In course of time their death and decay results in the formation of humus; silting adds to the increase in depth of soil and depth of water decreases. These reactions make the conditions better for the growth of other invaders.

(2) **Floating Stage**. As the depth of water becomes 2 to 3 metres anchored or free floating hydrophytes invade the area once

Fig. 6·3. Floating stage

occupied by submerged types. *Nelumbium, Eichhornia, Lemna, Pistia* are the common examples. Their leaves prevent light to reach submerged types, which either die or migrate to deeper layers. As years pass on these plants die. The intercepted soil particles are also deposited. These reactions result in further decrease in depth of water and thus render it unsuitable for their growth.

(3) **Reed Swamp Stage**. As the depth becomes less than even 1 metre the amphibious plants like *Typha, Saggittaria* and *Polygonum* make their appearance. These have rapid vegetative

Fig. 6·4. Reed Swamp stage

propagation like floating hydrophytes. They have vertical growing aerial leaves which shade the floating hydrophytes. Further addi-

tion of soil and their own death and decay adds to humus and reduction in the level of water to such an extent that it is just a few cm.

(4) Sedge Meadow Stage. Sedges and grasses belonging to Cyperaceae and Gramineae invade the areas now. By their reactions

Fig. 6·5. Sedge meadow stage

involving transpiration of large amounts of water, collection of soil around by intercepting wind and water carried soil particles. The soil becomes unfit now for the growth of hydrophytes.

Up to the end of this stage the reactions of the plants themselves were responsible for successions. Now further changes in the community are controlled by climatic factors. As soil becomes dry water will be made available by rainfall. Thus depending upon the climate the plants to follow may lead to grassland if the climate is dry. On the otherhand moist climate will produce woodland stage.

(5) Woodland Stage. Hydrophytic shrubs like willows (*Salix*), alder (*Alnus*), dogwoods (*Cornus*) make their appearance. Underneath

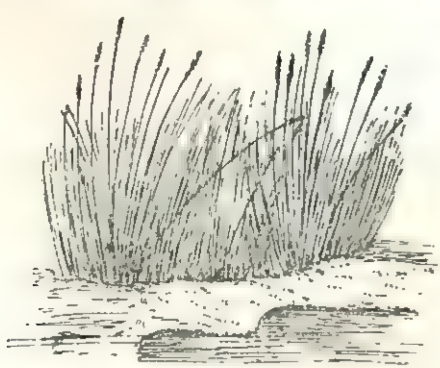


Fig. 6·6. Woodland stage

these, such herbs which are sciophytic, appear and grow as subdominants.

(6) Climax Forest. Depending further upon the climate the woodland stage may be made to give in favour of forest. In tempe-

rate climates mixed forests of Oak or Conifers may appear. In tropical climate with high rainfall, rain-forests develop. In drier

Fig. 6·7. Climax stage

climates deserts are formed.

XEROSERE

This represents the different stages in the development of succession on a rock or sand. The various stages are :

(1) **Crustose Lichens**. They are the first invaders to appear

Fig. 6·8. Crustose Lichen stage

on barren rocks. Their rhizoids penetrate into depression. The

acids secreted by them bring about chemical weathering of rocks to form soil. The common examples of these lichen are Lecanora and Rhizocarpon. They form extensive patches invading by means of soredia. Their death and decay forms small amounts of soil which becomes suitable for growth of foliose lichens.

(2) Foliose Lichens. They have leaflike appendages which cut off light from the crustose lichens making their growth impossi-

Fig. 6·9. Foliose Lichen stage

ble. The mechanical and chemical weathering of rocks is further facilitated. Their own death and decay adds to humus. Common examples are Dermatocarpon and Parmelia.

(3) Moss Stage. The humus and soil formed as a result of of reaction of Lichens is good place for the growth of xerophytic mosses which invade by means of spores. Their growth forms dense mats eliminating the lichens ultimately completely. Polytrichum and Grimmia are the first invaders as mosses.

Fig. 6·10. Moss stage

(4) Herbaceous Stage. The mosses generally form 3—5 cm layers of soil where annual xerophytic herbs make their appearance.

The mosses retain lot of moisture. This helps the seeds to germinate during rainy seasons. Penetration of roots in the crevices of rocks further adds to mechanical weathering and formation of soil. Depending upon the plants growing in surrounding communities the invading herbs are Potentilla, Solidago and Saxifraga. Their growth makes the conditions less drier. Bacteria, fungi and microfauna appear

Fig. 6·11. Herbaceous stage

along with grasses. Their death and decay further adds to the soil layers.

(5) Shrub Stage. Woody shrubs like Rhus glabra, or Rubus and Sassafras invade these areas. Their shade makes the growth of herbs impossible and thus they disappear. The humidity increases and wind velocity is decreased. The addition of organic matter to the soil increases water holding capacity of soil, its texture and structure is changed so that the seeds of trees find a suitable place for growth.

Fig. 6·12. Shrub stage

(6) **Climax forest.** The trees which make their appearance

first are dwarf sized, xeric and grow separated apart. They are however followed by mesophyte as the climate becomes more mesic. Quercus, Tilia are the common trees which find place in climax communities.

Fig. 6·13. Climax stage dominated by xerophytic shrubs

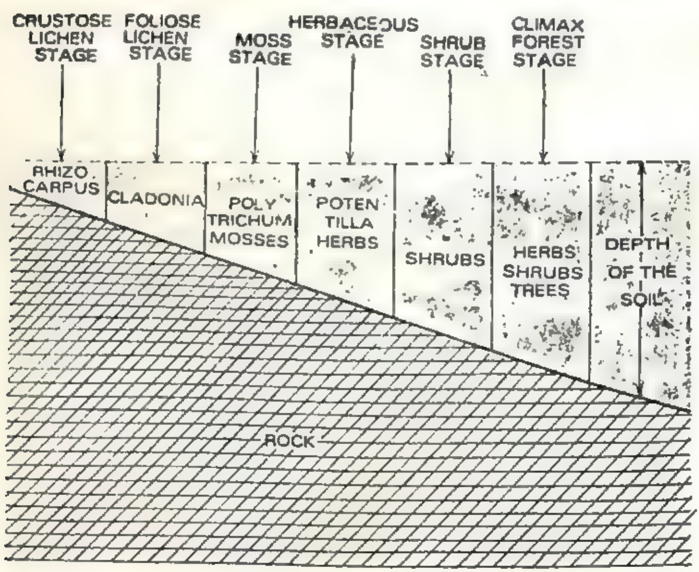


Fig. 6·14. Stages in a Xerosere

HALOSERE

When succession takes place in saline water like that of sea. Like hydrosere it supports the growth of halophytes which can flourish well in saline water. Mangroves like Rhizophora, Acanthus,

Avicennia, Aegiceras, Sueda, Ceriops, Bruguiera succeed commonly in halosere in the deltas of Ganga and Godavari.

Secondary Succession or Subseres

Secondary succession or subsere, develops in inhabited areas which have been modified by man or some other natural agency. It usually passes through fewer stages and it reaches the climax state more rapidly than the primary succession. The secondary succession

Fig. 6·15. A view of Mangrove vegetation dominated by Rhizophora, Sonneratia, etc.

may start on burnt lands, lumbered lands, or any secondary bare area from which the previous vegetation has been completely removed.

On a burnt land the secondary succession may start with annual grasses and other herbs. These may be replaced by perennial shrubs and trees. In due course of time the climax forest may be established.

From the above examples we find that succession whether starts on a rock or water ultimately ends into a mesophytic type of community. The initial stages are controlled by edaphic factors while final stages by climatic factors. Invaders migrate, germinate, grow, reproduce, make their own growth impossible and are overpowered by others. Thus waves of seral communities appear and

disappear till ultimately we find harmony between community and climate. Areas which had been shown as lakes in the past are dominated by large forests now. The knowledge about the principles of succession helps in the management of forest, wild life, agricultural lands etc.

QUESTIONS

1. What is plant succession ? Write an essay on plant succession.
2. What is sere ? Describe the various successional stages of hydrosere.
3. Describe the various development stages of pond studied by you. Give 4 examples of each stage.
4. Write short notes on the following :
   sere, causes of succession, climax; xerosere, secondary succession.

7

ECOLOGICAL FORMATIONS OF PLANTS ON WATER RELATIONS

Formation is the climax vegetation made up of one or more associations. It is controlled by environmental factors. The sum total of environmental conditions constitutes habitat. On the basis of water factor three types of habitats are recognised *viz.* Hydric, Mesic and Xeric. Hydric habitat is one where water is available in abundance, mesic in which normal supply of water is there and xeric is one where there is morphological or physiological dryness. In 1895 E. Warming classified the plants in these habitats as Hydrophytes, Mesophytes and Xerophytes respectively.

A. **Hydrophytes** are thus plants growing in regions where there is abundant supply of water *i.e.* in water, or in soils which practically remain saturated with available water throughout the year.

Some of the common hydrophytes and the families to which they belong are given below.

1. Ranunculus aquatilis —Ranunculaceae.
2. Nelumbium speciosum —Nympheaceae.
3. Nymphea lotus — ,,
4. Trapa bispinosa —Onagraceae.
5. Jussaea repens —Onagraceae
6. Utricularia species —Lentibulariaceae.

We can put these easily into five groups :—

(*a*) *Anchored submerged* :—These plants rooted at the bottom have their foliage submerged in water. These include *Ceratophyllum, Hydrilla, Vallisneria, Potamogeton, and Zanichellia.*

(*b*) *Suspended submerged.* These are not rooted at the bottom and remain suspended in the body of water. Forms like *Ceratophyllum* may lack roots later on and become suspended. *Utricularia, Lemna trisulca,* and many of algae belong to this group. In Utricularia floral shoots may come above the surface of water.

(*c*) *Anchored Floating* :—These are rooted in the soil but have their leaves floating on the surface of water. Typical examples are of *Nelumbium, Nymphea,* and *Marsilia.* In *Ranuculus aquatilis* leaves are dimorphic, submerged leaves are much dissected while aerial leaves are with normal palmate lamina.

(*d*) *Free Floating* :—They remain floating on the surface of water. Examples are *Lemna, Wolffia, Eichhornia, Salvinia, Riccia, Ricciocarpus, Pistia.*

(*e*) *Amphibious* :—These plants grow towards the periphery of body of water. Their underground parts are in water while leaves etc. are much above the water and distinctly aerial. Typical example is Typha. Forms like Polygonum, Saggittaria, Trapa have also partly submerged and partly aerial portions and may come as intermediate forms between anchored floating and Amphibious. These plants are also designated as Hygrophytes or Helophytes.

Morpho-physiological Characters of Hydrophytes :

External characters :

(*a*) Roots may either be altogether absent or are poorly developed. Root cap is absent. In its place they may possess root pockets which have probably balancing function. These become easily detached. Root hairs are either absent or poorly developed. Root shoot ratio is always less than one.

(*b*) Stem is herbaceous, offset, rhizomes are common which form extensive vegetative growth. Submerged stems are slimy. It is green with elongated internodes.

(*c*) Leaves in submerged forms are dissected, linear or linear lanceolate so as to offer least resistance to water currents. They too may be slimy. They possess practically no protective organs such as spines or thorns. Anchored floating types have long petioles bearing large leaves which float on surface of water. In Eichhornia, leaves have much swollen petioles, which help in floating. In Salvinia there are foliar adventitious floating roots. Ranunculus aquatilis shows dimorphic leaves or Heterophylly, floating leaves have waxy coating to avoid wetting. In Amphibious forms leaves are elongated and cylindrical.

Anatomical Characters :

(*a*) Vascular tissue specially the xylem is poorly developed. It may be completely absent and replaced by a central cavity as in Hydrilla.

(*b*) Ground tissue is parenchymatous with abundant air spaces making stem and leaves spongy in character. The aerenchyma helps in floating and internal circulation of air.

(*c*) Epidermal tissue system is not much developed. Cuticle may be thin or completely absent. Stomata are vestigial or altogether absent in submerged flora. They are restricted to dorsal surface in floating forms. Stomata are abundant in leaves of amphibious plants. Epidermal cells have chloroplasts.

(*d*) Mesophyll has practically no palisade tissue and is made up of spongy tissue.

In the case of amphibious type like Typha we find that internal structure has mechanical conducting tissue developed side by side with aerenchyma. They show characters in between hydro- and mesophytes or even xerophytes as the soil may sometimes be depleted of water during a small period of year.

Physiological Characters

(*a*) Absorption is through general surface in the case of submerged forms and through roots in anchored floating and amphibious forms. Osmotic Pressure of Cell sap is low.

(*b*) Transpiration stream is poor in submerged types while amphibious forms have well developed transpiration stream.

(*c*) Photosynthesis releases oxygen and respiration CO_2 which have internal circulation through air spaces. O_2 is stored during day time and CO_2 during night hours. Photosynthesis is poor as Quality and intensity of Light is effected when it penetrates through water.

(*d*) Vegetative reproduction is prominent and seed formation poor.

(*e*) Plants when taken out of water wilt rapidly as compared to xerophytes.

B. Xerophytes :—These are the plants of Xeric habitat. Xeric habitat may be the result of poor water holding capacity of soil, or water is in abundance but presence of salts or lack of aeration creates non-availability to plants. Solar radiation increases the loss of water by transpiration or evaporation.

List of Representative types of Xerophytes with their families is given below before discussion of their characters.

1. Calotropis procera—Asclepiadacea. (Ak)
2. Capparis aphylla—Capparidaceae. (Karir or Dela)
3. Aloe vera—Liliaceae. (Kanvar gandal)
4. Agave americana—Amaryllidaceae
5. Yucca aloefolia—Liliaceae (Chittar Thor)
6. Opuntia species and other Cactii—Cactaceae.
7. Zizyphus numularia—Rhamnaceae. (Malah)

These can be put under 5 types

(*a*) *Drought Escaping* or drought avoiding Annuals or Ephemerals. They complete their seed formation in short time and thus tide over unfavourable dry periods in the form of seeds. These seeds germinate quickly at the time of rainy season *e.g.* Carthamus oxycantha Argemone mexicana.

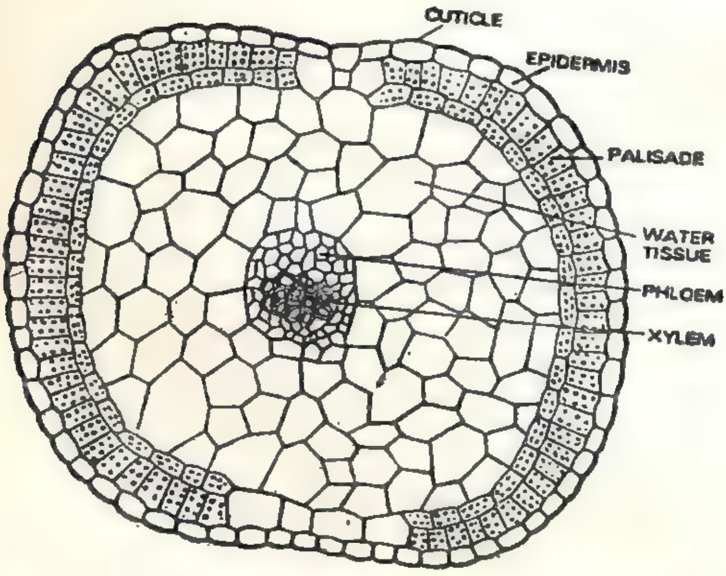


Fig. 7.1 T.S. through leaf of *Salsala*. Note central water storage tissue Peripheral palisade tissue.

(*b*) *Succulents.* They store water during short span of rainy season and use it during drought period. Roots are succulent in Ceiba parvifolia ; stems in Opuntia, Euphorbia royleana, and various cactii, leaves in Agave and Aloe.

(*c*) *Drought Resistant* or True Xerophytes :—These plants have various modifications to withstand xeric conditions. These include

(*i*) maximum absorption of water (*ii*) minimum transpiration (*iii*) Mechanical tissue to avoid wilting.

Calotropis procera, Capparis aphylla, Zizyphus nummularia, etc. are common examples.

(*d*) *Halophytes.* These are the plants which grow in areas where there is physiological dryness. The soil is physiologically dry

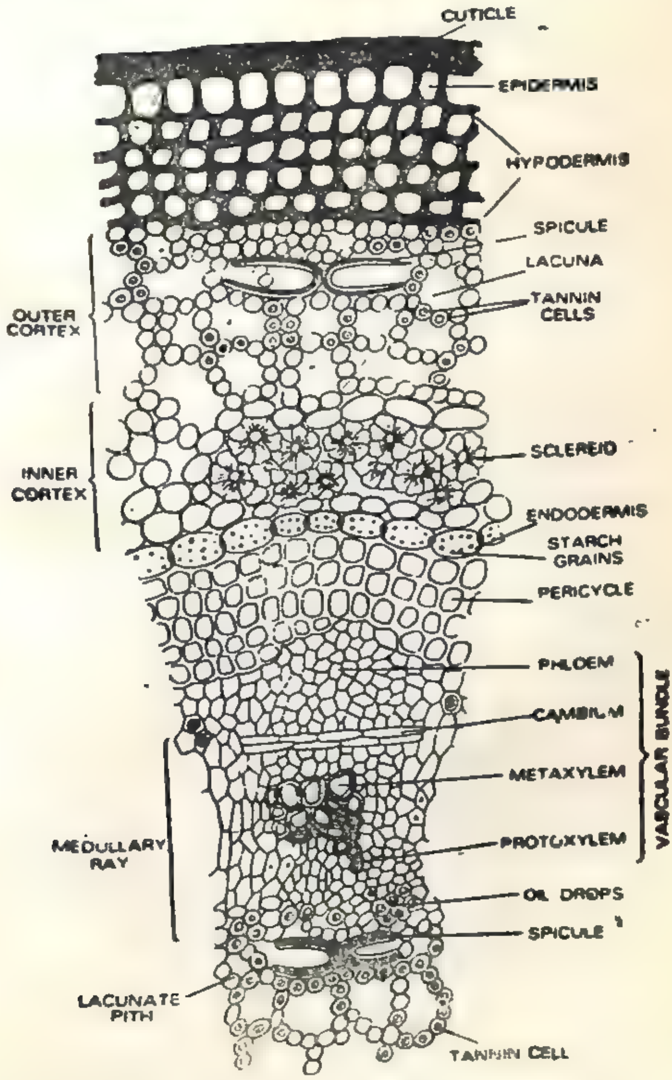


Fig. 7.2. T.S. Stem of *Rhizophora.*

when water is not available either due to higher concentration of salts *e.g.* saline soils or due to poor aeration of soils *e.g.* marshy areas.

Salsola foetida Sueda fruticosa, Atriplex are the plants of saline soils Rhizophora of marshy places. Plants of marshy places are also called as mangrove plants. They possess two chief characteristic features. Firstly they have pneumatophores or breathing roots which come above the soil surface and possess lenticels. Secondly they have the feature of vivipary *i.e.* shed their seeds in semi-germinated condition. These seedlings are able to establish easily.

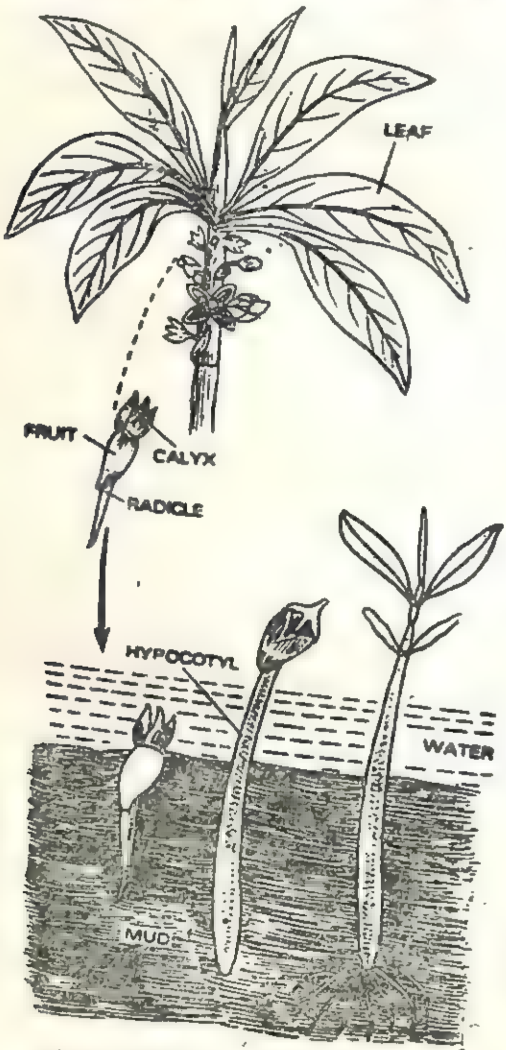


Fig. 7·3. Vivipary in *Rhizophora*

(e) *Alpine Plants.* These plants inhabit the higher altitudes, strong intensity of light and blowing winds, poorly retained water

due to slopes make the conditions xeric. Low temperatures falling below freezing point become a factor of hindrance in absorption of water. Rhododendron, Saxifraga, Potentilla are the common examples. According to Puri, Indian Alphine vegetation has three subtypes (*i*) Alpine stony desert (*ii*) alpine scrub and (*iii*) alpine pasture. The first forms rocky slopes below snow line, Lichens, Sedum, Primula form the main flora. The second group is represented by flora

Fig. 7·4. A few forms of cacti possessing succulent stems for living under xerophytic conditions

of Rhododendron anthopogon and Salix sclerophyla. The third group is above the scrub zone. The flora here is characteristically dwarf. Members of Ranunculaceae *e.g.* Anemone, Aconitum and Aquilegia may be mentioned.

General Characters of Xerophytes :

External Characters

(*a*) **Roots.** They possess well developed root system. The root shoot ratio is always more than one. Many perennials have elongated tap roots which may reach deep layers of subsoil which is usually moist due to water table. Root hairs are abundant. Root caps are present. They may have the feature of rapid elongation as water recedes.

(*b*) **Stem.** The stems become green and take up the function of photosynthesis in cases where leaves fall off or are absent. Phyllo-clades is the name given to such stems which become flattened and

leaf like as in Ruscus and Asparagus. In Opuntia phylloclade is succulent due to storage of water. In capparis green stem carries on photosynthesis as it becomes leafless. Stem spines are common. Stems may have mealy surface, waxy or hairy coating. The internodes are small.

(c) **Leaves.** The leaves may be altogether absent or modified to form scale or spines. In Australian Acacia the lamina falls off and petiole becomes flattened to form Phyllode. The leaf lamina is reduced and plants are microphyllous. However, it may be mentioned here that microphylly has nothing to do with reduction of transpiration. Leaves have shining surface, dull grey appearance, mealy or waxy coating, hairy or spiny surface and margin. The lamina show folding or rolling—common in legumes and grasses respectively. In Euphorbia splendens the leaves make their appearance during rains and are shed as soon as soil dries up. Leaves become vertically oriented so as to reduce the effect of light radiation. The leaf margins become permanently revolute. All these adaptations are to withstand wilting, reduce transpiration, and afford protection against herbivores.

Anatomical Characters

There is general reduction in cell size, may be of roots, stems or leaves. This is due to poor hydration.

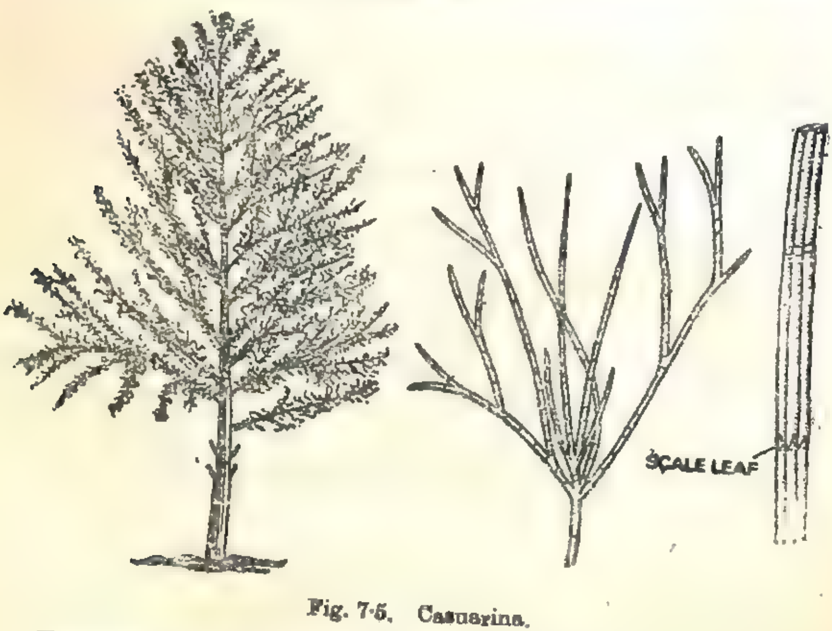


Fig. 7·5. Casuarina.

Epidermal tissue system is well developed. Epidermal cells

develop highly thickened cuticle. May have waxy or hairy coating outside. In Nerium epidermis is multi-layered in leaves. The stomata may be sunken in position or lie in cavities surrounded by hairs. This avoids direct contact of internal air with external air.

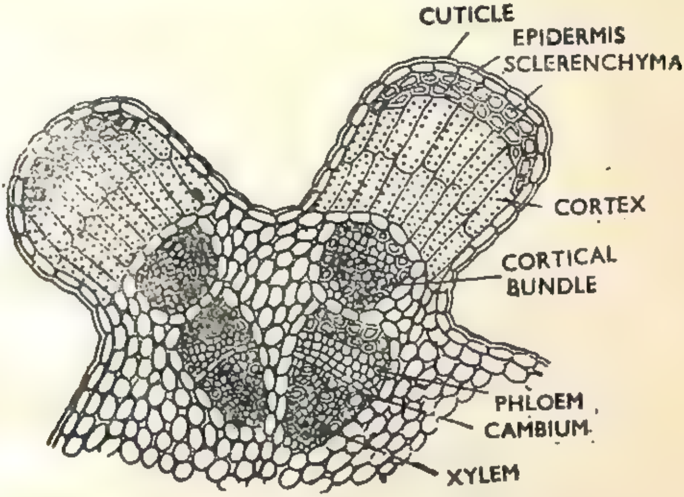


Fig. 7·6. T.S. portion of *Casuarina* Stem

Ground tissue system has abundant sclerenchyma. There may be well developed sclerenchymatous hypodermis. Sclerencphymatous

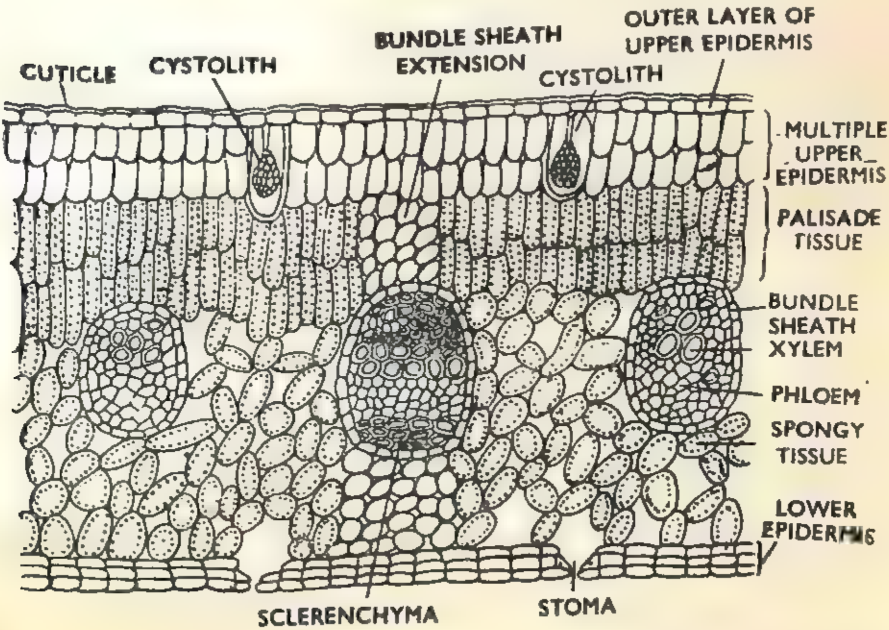


Fig. 7·7. T.S. Leaf *Ficus benghalenses*

pericycle in stems. Both these features explain sclerocauly and sclerophylly, found in leaves. In leaves mesophyll has well developed palisade tissue.

Vascular tissue system is well developed. Xylem and phlöem are well developed. Lignification starts earlier and makes Xylem elements well developed. Leaves have transfusion tissue which compensates for the absence of lateral veins.

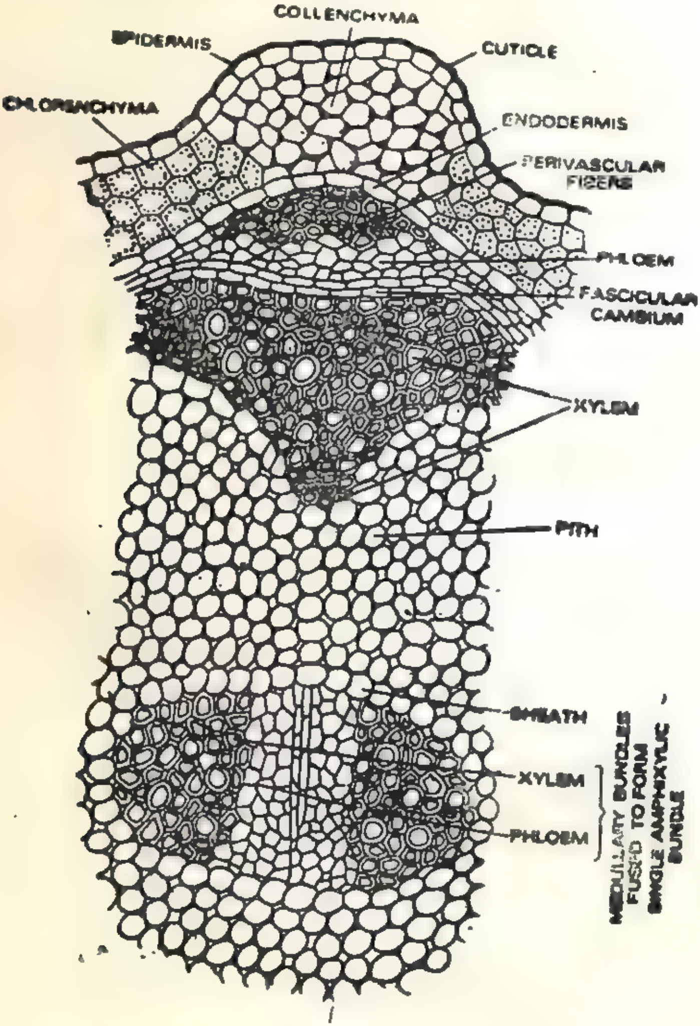


Fig. 7·8. Stem *Achyranthes asper*. Note the fused medullary bundles.

Physiological Characters

Cell sap has high Osmotic Pressure. The highest being found in halophytes.

Transpiration is more in Xerophytes than in mesophytes when both are placed in sufficient available water. However, under permanent wilting conditions the transpiration is greatly reduced in xerophytes than in mesophytes. Sclerocauly and Sclerophylly prevent breakage during wilting.

Succulence may arise due to drier conditions, water content being low, polysaccharides are converted into pentosans. The pentosans with nitrogenous compounds get highly hydrated. The reactions being irreversible result in succulence. They have latex or resins or oils.

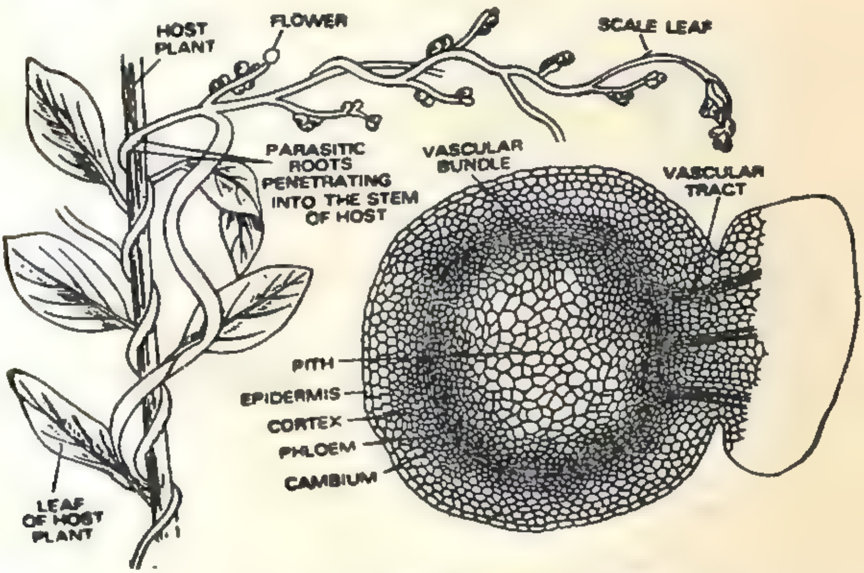


Fig. 7·9. *Cuscuta*

In the succulent cactii the stomata remain closed, the food is oxidised to form organic acids and then CO_2. Carbon dioxide is utilised in photosynthesis.

Formation of fruits and seeds is more favoured than vegetative reproduction.

In nature xeropyhtes are more abundant than hydrophytes. Their characters also are so variable that it is difficult to generalise. Sometimes quite contrasting characters may be present in plants growing under similar xeric environment. In fact each plant seems to have solved its problem in its own way.

Plants growing on rocks and stones are called as **lithophytes** or Petrophytes. Those growing on sand are called **Psammophytes**.

Coniferous forests which are ever green and grow at high altitu-

des where climate is cold are put under **Psychrophytes**. **Oxylophytes** are the plants which grow on acid soils.

Mesophytes. They are the ordinary land plants which grow in habitats that are neither dry nor moist. They form the major portion of vegetation in the world. Their characters are the characters of ordinary land plants which are in between the hydrophytes and xeropoytes. However, a few of general characteristics

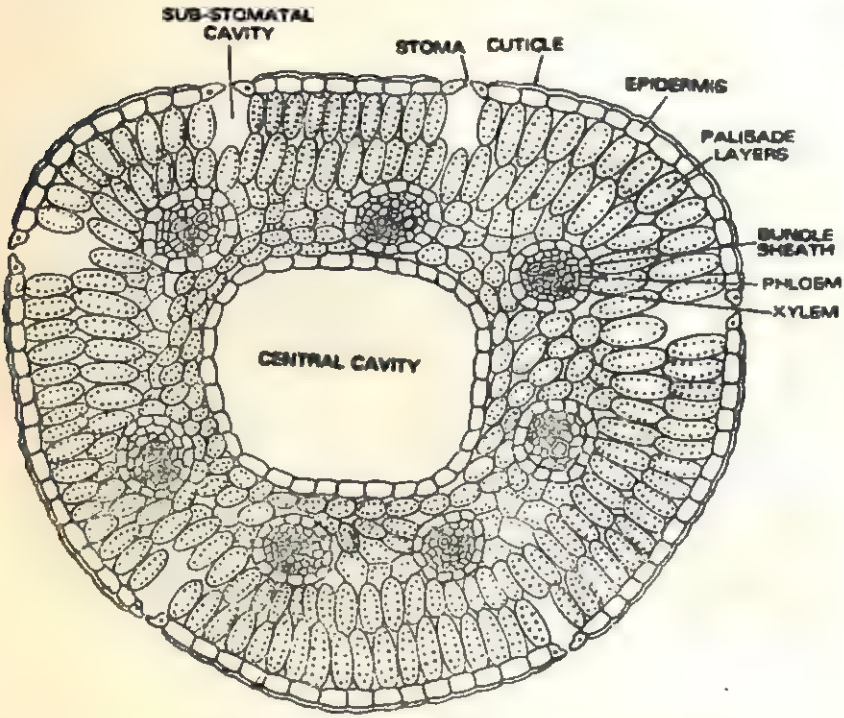


Fig. 7·10. T.S. Leaf *Allium cepa (onion)*

may be summed up for recollection of what readers have studied about them. Root shoot ratio is nearly one. Amongst dicot and gymnosperms tap root system is prevalent while in Monocots and Pteridophytes it is usually adventitious root system. The shoot system bears an extensively developed foliage. The leaves are thin and large. The cuticle being thin they appear dark green at least on the dorsal side. Both vegetative and reproductive growth is carried on. There is normal development of epidermal tissue system with abundant stomata, vascular tissue system with xylem and sclerenchyma equally distributed. The osmotic pressure of cell sad is neither high nor low.

According to light requirements they may be classified as **Sciophytes** and **Helophytes**. Sciophytes are plants which grow normally in shady areas. Submerged hydrophytes, majority of Epiphytes and sub-dominants growing under dominant trees and shrub associations are examples of sciophytes.

QUESTIONS

1. What are hydrophytes ? Describe the various morphological and anatomical adaptations met within hydrophytes.

2. Describible the various features of different groups of hydrophytes. Illustrate your answer with suitable examples.

3. What are xerophytes ? Describe the various morphological and physiological adaptations of xerophytes.

4. Describe the main ecological adaptation of plants growing in water ponds.

5. Write short notes on the following :

Succulents, Amphibious plants, Heterophylly, Sclerophylly, Bulliform cells, Trichophylly, Diaphragm.

8

EPIPHYTES

(*Epi*=above, *phyton*= plant, *i.e.*, plant growing upon plant)

Epiphytes are those autotorphic plants which grow on the surface of some other supporting plants and are not permanently rooted in the soil. Orchids, Bo tree (Pipal tree), some algae, lichens and mosses are some of the familiar examples. These plants absorb sufficient moisture from the atmosphere and mineral nutrients from the decaying bark of the supporting plants upon which they are situated. As they are autotorophic in nutrition, they manufacture their own food (carbohydrates) from water and CO_2 in presence of sunlight. These plants differ from parasites because they do not derive nutrients and water from the living parts of supporting plants, and also they differ from lianes (woody stem climbers) because epiphytes, in the real sense of the term, are not permanently rooted in the soil. Epiphytes are also called *Aerophytes* or air plants.

Distribution

Some epiphytes grow on the surface of submerged aquatic plants, while others may be aerial. Some are found growing on the surface of tree trunks, some on the horizontal forks of the trees and some may grow even on the surface of leaves (*i.e.*, epiphyllous epiphytes). Some epiphytes show specificity in selection of their supporting plants. *Tortula pagorum*, an epiphytic moss, is peculiar in the sense that it grows on the tree trunks within the urban limits. This moss grows well in the city atmosphere presumably because it requires high temperature and smoky air for its normal growth. Both these factors are available to the plants in the city area. Some

epiphytic species may often grow on rocks. and some may grow rarely even on the poles and horizontal telephone wires.

Epiphytic vegetation is very rich in moist and cold regions but poor in dry and cold areas. In north-western Himalayas the epiphytic species are much less in number in comparison to those present in the eastern Himalayas. In warm and wet regions, members of the families Bromeliaceae and Orchidaceae are found in abundance. In tropical rain forests, epiphytic species found at the tops of trees are xerophytic in nature but those occurring at lower levels are hygrophilous (moisture and shade loving).

Important Features

Since the epiphytes depend directly for their water supply on rains, atmospheric moisture, snow and dew, they develop certain structural adaptations for water storage and for reducing excessive water loss. The important features are listed below :

1. Morphological Features

(i) **Root System**. In the epiphytic vascular plants, the root system is extensively developed. In these cases, the roots may be of the following three types (Fig. 8·1) :

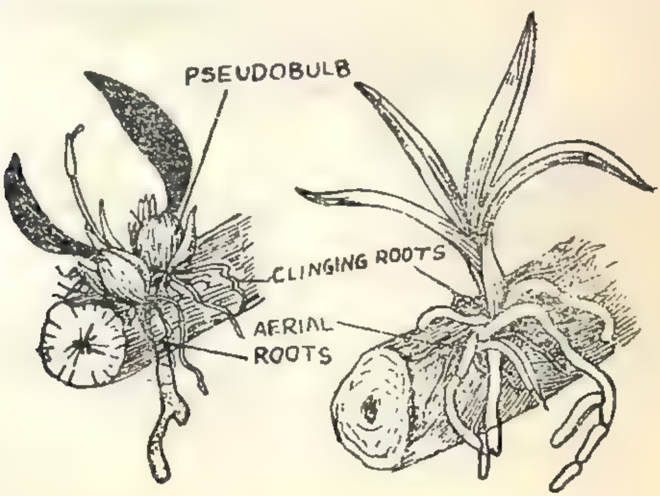


Fig. 8·1. Different types of roots in epiphytes.

(a) **Normal Absorbing Roots**. Which absorb water, minerals, and organic nutrients from the moist crevices of decaying barks of supporting plants.

(b) **Clinging Roots**. These roots fix the epiphytes on the surface of the supporting object firmly and also absorb nutrients from the humus and dust that are accumulated on the surface of the bark.

(c) **Aerial Roots**. These are spongy and green roots which hang downwardly in the atmosphere and absorb moisture from the air. These roots can photosynthesize in light because of the presence of green colour in them.

In some epiphytes, the roots collect on their surface good amount of dust that holds water which will finally be absorbed by the roots.

(ii) **Stem**. Stem in epiphytic vascular plants may or may not be extensively developed. Some epiphytes develop succulence in their stems and become pseudobulbous or tuberous (Fig. 8·1).

(iii) **Leaves**. The majority of epiphytes show considerable reduction in leaf number. Some orchids develop only a single leaf in a growing season. Leaves in some may be fleshy and leathery. In *Dischidia nummularia*, *Platycerium* and *Asplenium nidus* leaves are modified into the pitchers.

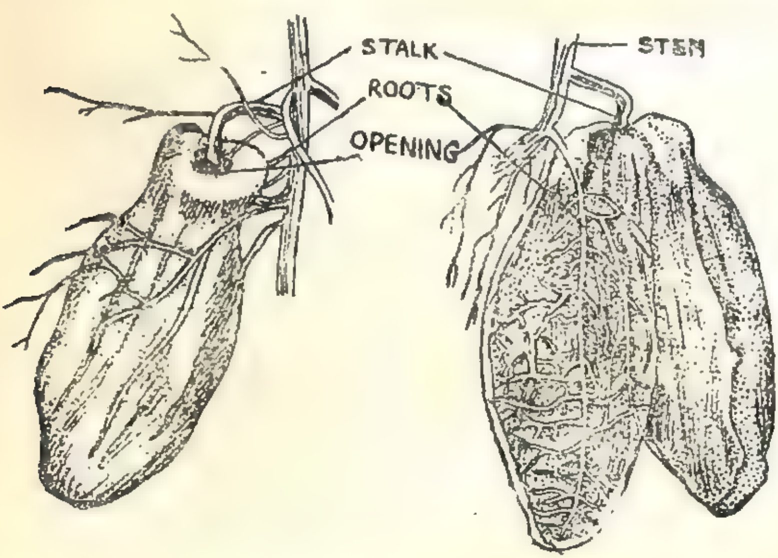


Fig. 8.2. Leaf pitchers of *Dischidia nummularia*. Right pitcher is cut open longitudinally to show network of roots on its inner surface.

Dischidia nummularia, an epiphytic species of family Asclepiadaceae, growing very commonly in Sunderban shows peculiar

type of leaf pitchers. The pitchers have openings through which the adventitious roots enter inside. The roots branch copiously into a number of very delicate rootlets which spread on the entire inner surface of pitcher and form a network (Fig.8.2.).The inner surface cf pitcher is coated with wax. Pitcher collects and accumulates rain water, humus and minerals that are absorbed by the root network. Sometimes ants and insects enter the cavity of the pitcher through hole where they may be killed and digested. The dead remains of animals serve as nitrogen sources for the plants· Myrmecophily which is a sort of symbiotic association bitween ants and plants is of common occurrence in the epiphytic vegetation. In the family Bromeliaceae, some species develop spoon-like leaves in rosettes. These leaves collect and store rain water which is finally absorbed by the epidermal hairs present on the concave surface of the leaves.

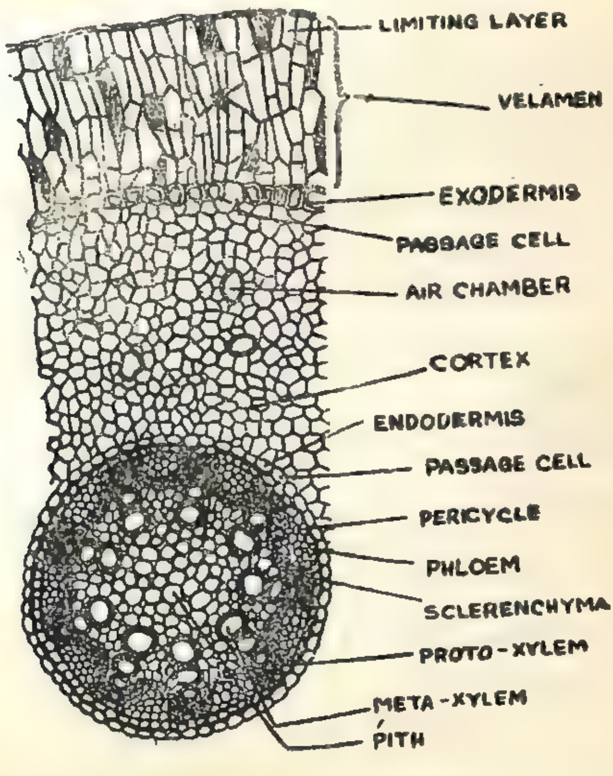


Fig. 8.3. T.S. of aerial root of orchid showing velamen.

(iv) Fruits, Seeds and their dispersal. The fruits and seeds are usually dispersed by wind, insects and birds. When the

seeds reach the suitable surface and get favourable environment, they germinate over there and give rise to new independent epiphytes

2. Anatomical Features

Important anatomical peculiarities in epiphytes are as follows :

(*i*) Presence of thick cuticle and sunken stomata : These two structures greatly reduce the loss of water from the plants. Generally the surface cells of water absorbing organs (roots and some leaves) are not cuticularized.

(*ii*) In succulent epiphytes, thin-walled parenchymatous tissue that stores water, develops extensively.

(*iii*) The aerial hanging roots of many tropical epiphytes belonging to the families Araceae and Orchidaceae develop on their surface a characteristic greenish white, thin-walled massive tissue that is called velamen (Fig. 8.3). The velamen is hygroscopic tissue that rapidly absorbs moisture from the saturated atmosphere like a sponge. It is modification of multilayered epidermis. Its cells are empty (*i.e.*, dead) and cell walls show spiral or reticulate thickenings. Inner to the velamen there is present a peculiar layer called *exodermis*. Exodermal cells are of two types :

(*a*) Lignified and thick-walled cells.

(*b*) Thin-walled cells or passage cells, walls of which are permeable to water. The velamen absorbs and retains moisture till that is absorbed by passage cells of exodermis.

(*iv*) Other structures are similar to those found in mesophytes.

Types of Epiphytes

Schimper has classified epiphytes into four subgroups which are as follows :

(1) **Protoepiphytes**. These plants derive their nourishments partly from the surface of the supporting plants and partly from the atmosphere. They do not develop any adaptive feature in them except, perhaps, aerial roots with velamen. Examples : *Peperomia*, *Dischidia* and some ferns belong to this group.

(2) **Hemiepiphytes**. These plants grow on the supporting plants in the beginning like true epiphytes but later on they establish connection with the soil by their roots. Epiphytic fig trees, some root climbing Aroids, *Scindapsus officinalis* etc. are important

Some stem climbing plants grow in the soil but their stems die

from below upward and terminal portions live independently like hemiepiphytes. Such plants are termed as Pseudoepiphytes.

(3) **Nest epiphytes**. These plants have appropriate devices to collect large quantity of water and humus for their own use, orchids are familiar examples of this group.

(4) **Tank epiphytes**. These plants develop fibrous anchoring roots which do not take part in the water absorption. Leaves, that are variously modified, absorb water and manufacture food. *Nidularium*, *Tillandsia*, and other epiphytic species of Bromeliaceae are common plants of this group.

QUESTIONS

1. What are epiphytes ? Describe the various morphological features of epiphytes.

2. Write short notes on:

(*i*) Velamen (*ii*) Root system of epiphytes.

9

HALOPHYTES AND MANGROVE VEGETATION

Some plants grow and complete their life cycle in habitats with a high salt content. They are known as salt plants or halophytes. According to Stocker (1933), the critical level of salinity for plants is 0.5% of the dry weight. Though the fact that only a small group of higher plants can grow in the saline habitats was recognized many hundred years ago, yet the name "halophyte" was assigned to such plants by Pallas in the early nineteenth century. Such plants are commonly found near sea shores where mesophytes and fresh water hydrophytes can not thrive well. Although these plants grow in the areas which are well saturated with water yet they cannot avail of the water because of high concentration of salts in the soils. Thus, the halophytes are plants of physically wet but physiologically dry habitats. Plants cope with the problems of salinity in various ways, some of them avoid salinity, some evade salinity or resist it, and a few others tolerate salinity. Salinity avoidance is usually accomplished by limiting germination, growth and reproduction to specific seasons of the year as well as by growing roots into non-saline layers and limiting salt uptake. Plants evade or resist salinity by accumulating salts in their cells as well as by secretion of excess salts. In the salt tolerants, the protoplasm functions normally and endures a high salt concentration without apparent damage.

Classification of Halophytes

Stocker (1933) proposed first classification of saline habitats which is as follows :

1. Aquatic-haline
2. Terrestro-haline
   (*a*) hygrohaline
   (*b*) mesohaline
   (*c*) xerohaline
3. Aero-haline
   (*a*) Habitats affected by salt spray (maritime)
   (*b*) Habitats affected by salt dust (salt desert)

Mangrove plants are very commonly found on some saline soils of Indogangetic plains (Bay of Bengal, Sunderbun and Assam), in Western India near the sea coasts of Bombay and Korala, in the banks of Gaumati and Godavari in South India, particularly in the regions where rivers meet the ocean, and in Andaman and Nicobar Islands.

Mangrove vegetation of Gangetic estuary, particularly of Sundarbun region, according to Prain, are localized in the following three georaphical zones :

(1) Southern coastal strip and south-western part
(2) Central zone
(3) North-eastern part

The Central zone is characterized by climax forest of *Heritiera Ceriops* is one of the dominant plant species on the higher grounds near the sea and at certain places it may form pure forest in Sunderbun.

Mangrove vegetation in the western sea coast of India is represented by the following plant communities .

(*i*) *Avicennia alba* and *Avicennia officinalis* community,
(*ii*) *Acanthus ilicifolius* and *Avicennia alba* community,
(*iii*) *Suaeda fructicosa* population,
(*iv*) Pure community of *Salvadora* species,
(*v*) *Sesuvium portulacastrum* population, and
(*vi*) *Aeluropus repens* population.

Godavari delta in Andhra (South India) shows characteristic mangrove vegetation of *Avicennia alba*, *Avicennia marina*, *Rhizophora*, *Bruguiera*, *Ceriops*, *Sonneratia*, *Acanthus ilicifolius*, *Myriostachya weightiana*, *Clerodendron inerme*, etc.

The ecological conditions which are essential for development of mangrove vegetation or halophytes are :

(*a*) shallow water with thick mud,

(*b*) water logged saline soil or sandy or loose soil or heavy clays containing large amount of organic matter,

(*c*) high rainfall, and

(*d*) high humidity in the atmosphere and cloudy weather.

Important Characters of Halophytes

As the water in the habitat is not such that can easily be absorbed by the plants, the halophytes develop almost all important xerophytic devices in them for water economy.

1. **Habit**. A great majority of halophytes in the tropical and subtropical regions are shrubs, but a few of them are herbaceous, for example, *Acanthus ilicifolius*. In temperate zones, halophytic vegetation is purely herbaceous.

The shrubs are generally dome-shaped in appearance because of their cymose branching.

2. **External morphology**. **(a) Roots** (*i*) Halophytes develop many shallow normal roots. In halophytes, in addition to normal roots, many stilt or prop roots develop from the aerial branches of stem for efficient anchorage in muddy or loose sandy soil. These roots grow downwardly and enter the deep and tough strata of the soil. In some plants, *e.g.*, *Rhizophora mucronata*, the stilt roots may be strong and extensively developed, but in others they may be poorly developed (*Rhizophora conjugata*). In some plants, the stilt roots may not at all develop.

(*ii*) Sometimes, a large number of adventitious root buttresses develop from the basal parts of tree trunks. These root buttresses provide sufficient support to the plants.

(*iii*) The soil in coastal region is poorly aerated and it contains very little percentage of oxygen because of water logging. Under such conditions, the roots of halophytes do not get sufficient aeration. In order to compensate this lack of soil aeration, the hydrohalophytes develop special type of negatively geotropic roots, called '*pneumatophores*' or breathing roots (Fig. 9.1). The pneumatophores usually develop from the underground roots and project in the air well above the surface of mud and water. They appear as peg-like structures. The tips of these respiratory roots may be pointed. They possess numerous lenticels or pneumathodes on their surface and prominent aerenchyma enclosing large air cavities internally. The gaseous exchange takes place in these roots through the lenticels. The aerenchyma helps in the conduction of air down to the subterra-

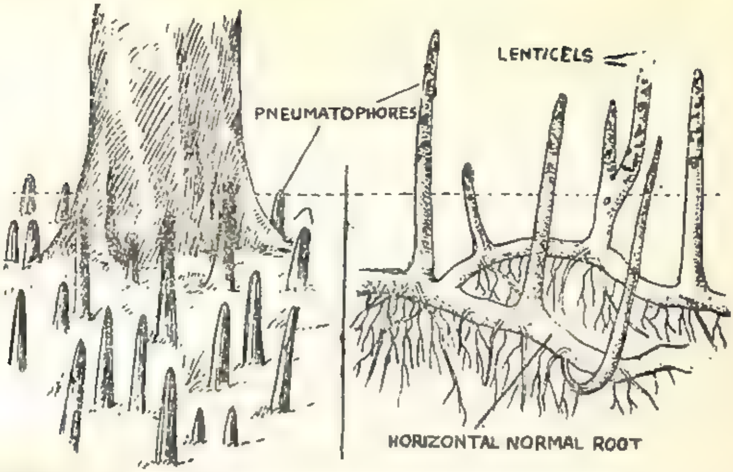


Fig. 9.1—Pneumatophores of mangrove plant.

nean or submerged roots. In some plants, *e.g. Bruguiera*, the horizontal roots grow above the surface of mud and then again bend

Fig. 9.2—Supporting or stilt roots of mangrove plants developing from the trunk.

downwardly and enter deep in the mud. In this way, they form knee-like structures. The aerial surface bears a number of pores

which facilitate the exchange of gases (Fig. 9.2). Pneumatophores do not develop in some species of *Rhizophora*. In those cases, the upper aerial parts of descending stilt roots probably take up the respiratory activity.

(*b*) **Stem**. Stems in several halophytes develop succulence. *Salicornia herbacia* (Fig. 9.3), *Suaeda maritima* may be quoted as familiar examples for it. According to Arnold (1955), the succulence depends on the ratio of absorbed to free ions in the plant cells rather than absolute amounts of sodium, chloride. or sulphate present. Succulence is induced only after the accumulation of free ions in an organ increases above a critical level. According to Pokrovskaya (1954, 57) salinity inhibits the cell division and stimulates cell elongation. Such effects cause decrease in the cell number and increase in cell size, so typical of succulents. Repp *et al* (1959) are of the opinion that succulence is directly correlated with salt tolerance

Fig. 9.3—*Salicornia herbacia*, a succulent halophyte.

of plants and the degree of their development can serve as an indicator of the ability of plants to survive in highly saline habitats. The temperate halophytes are herbaceous, but the tropical ones are mostly bushy and show dense cymose branching. Submerged marine angiosperms are among the very few species of halophytes that do not become succulent.

(*c*) **Leaves**. The leaves in most of the halophytes are thick, entire, succulent, generally small sized, and are often glassy in appearance. Some species are aphyllous. Stems and leaves of coastal aerohalophytes show additional mode of adaptation to their habitats. Their surfaces are densely covered with trichomes.

Leaves of submerged marine halophytes are thin, and have very poorly developed vascular system and frequently green epidermis. They are adapted to absorb water and nutrients from the medium directly.

(*d*) **Fruits, Seeds and their dispersal**. The fruits and seeds are generally light in weight. Fruit walls have a number of air chambers and the fruits, seeds, and seedlings which can float on the water surface for pretty long time are dispersed to distant places by water current. Mangrove vegetations of tropical sea shores from Australia to East Africa include approximately the same species of plants. Similarly, the mangroves of West Asia show considerable resemblances with those of East Asia and East Africa. It is due, in part, to the fact that medium and temperature remain uniform throughout and partly due to the efficient means of dispersal or migration of plants. A littoral species of *Spinifex* (*S. quarrosus*), a member of Graminae commonly growing in the sandy saline sea shores in Andhra, shows peculiar type of fruit dispersal. In this

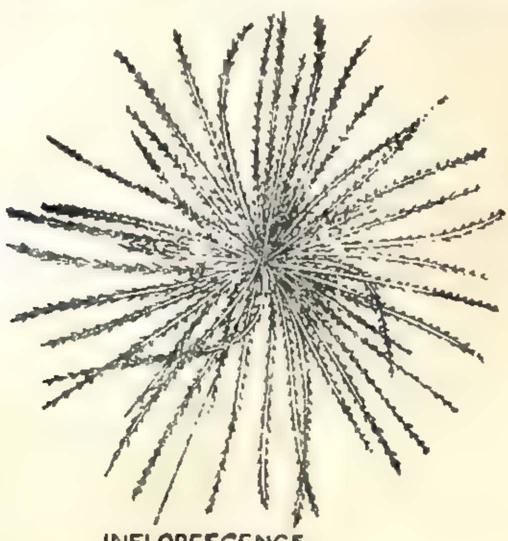


Fig. 9·4. Inflorescence of *Soinifex quarrosus*

plant, female inflorescence is spherical in shape and consists of many spikelets (Fig. 9.4). A number of stiff bractiolar bristles of the inflo-

rescence help in the dancing and somersaulting of the inflorescence. When the seeds mature the globular and hairy inflorescence becomes bodily detached from the creeping plant and trails on the sandy

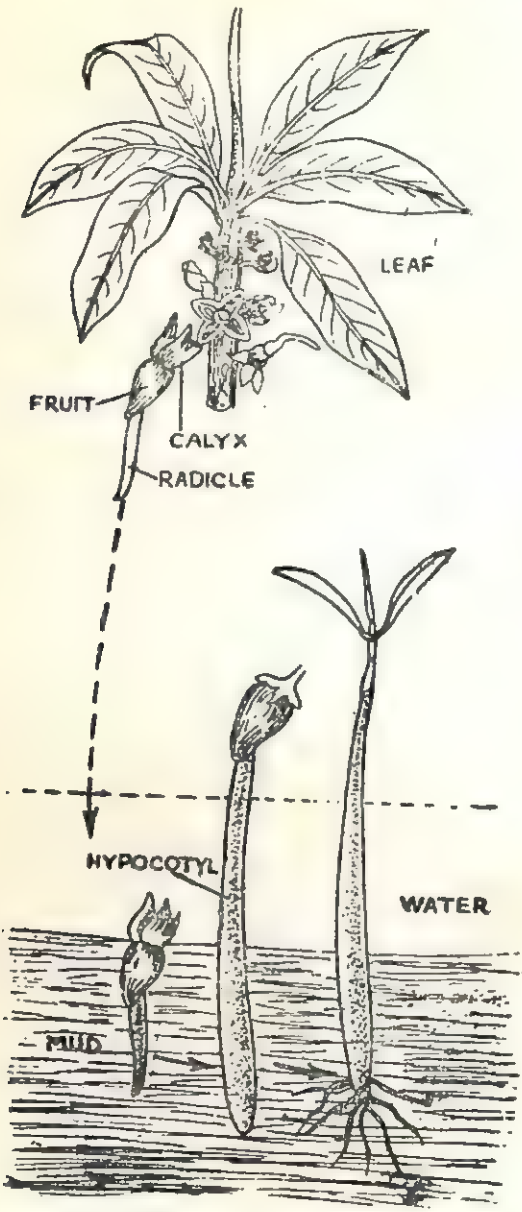


Fig. 9·5. Vivipary in *Rhizophora*.

substratum dropping its seeds at places. Finally the inflorescence with rest of fruits becomes buried in the mud.

(*e*) **Viviparous mode of seed germination.** Halophytes or mangrove plants growing in the tidal marshes are met with the phenomenon of 'vivipary' which is defined as the germination of seeds while the fruits are still attached to mother plants (Fig. 9.5).

In *Rhizophora* plants, when the embryo reaches to advanced stages of development the massive club-shaped hypocotyl and terminal radicle pointing downwardly emerge out of the fruit. When the hypocotyl attains a length of several centimetres (about 50-80 cms), the seedling falls vertically down. Thus, the radicle and a part of hypocotyl alongwith other embryonal parts, such as plumule and cotyledons remains above the surface of mud or water. Within a few hours the radicle develops a tuft of roots and plumule also starts growing rapidly. Sometimes seedlings fall in deep water and they float on the surface of water vertically with hypocotyl pointing downwards. On reaching to shallow areas, the radicle becomes fixed in the soft mud and the plant starts growing very rapidly. It is noticed that high degree of salinity in the soil or water checks the germination of seeds. So the viviparous germination is a very significant adaptation in these plants to avoid the retarding effects of salinity on seed germination. Species of *Rhizophora, Aegiceras, Avicennia, Cassula, Ranansatia vivipara* are some of the common examples for vivipary.

3. Anatomical Features

The appearance and structures which characterise a certain growth of plants sum up to a great extent their ecological and physiological means of adaptation. Halophytes are no exception to this rule because of specific and typical structural characteristics which make them distinguishable from other groups of plants. These are:

1. Large cells and small intercellular spaces
2. High elasticity of the cell walls
3. Extensive development of water storing tissues
4. Smaller relative surface area (surface/volume ratio)
5. Small and fewer stomata
6. Low chlorophyll content.

Anatomy of halophytes reveals a number of xerophytic features in them. These are as follows :

(*i*) Presence of thick cuticle on the aerial parts of the plant body. The epidermis of xerosucculents and coastal halophytes is characterized by a cover of waxy layers in addition to thick cuticle (Uphof, 1941).

(*ii*) Leaves may be dorsiventral or isobilateral. They develop protected stomata which are not deeply sunken. Epidermal cells are thin-walled. The palisade consists in several layers of narrow cells with intercalated tannin and oil cells.

(*iii*) Stems in the succulent plants possess thin-walled water storing parenchyma cells in them. Mucilage cells may be found in abundance. Epidermal cells of various mangrove species contain large quantities of tannins and oil droplets. Cortex is fleshy, several cells thick and in old stems it may become lacunar. Salinity causes extensive lignification of stele.

(*iv*) The leaves and stems of coastal halophytes are abundantly covered with various types of simple and branched trichomes, giving the plants a greyish appearance. The trichomes may exert a protective function in plants by :

(*a*) affecting water economy.

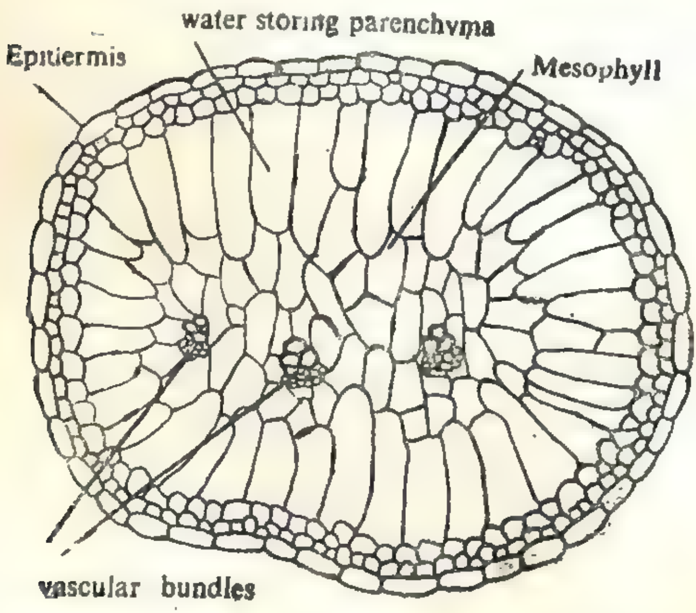


Fig. 9·6 A—T.S.of succulent *of Suaeda monoica* showing water storing parenchyma

(*b*) affecting the temperature of their leaves, and

(*c*) preventing sea water droplets from reaching the live tissues of leaves.

(*v*) Leaves of many species of mangrove are dotted with local cork formation "cork warts". Leaves of *Sonneratia* and *Aegiceras* and *Nitraria* (a desert shrub), *Suaeda monoica* contain well developed aqueous tissue (Fig. 9.6A) (Mullan, 1932). Salt secreting glands may be found in some halophytes.

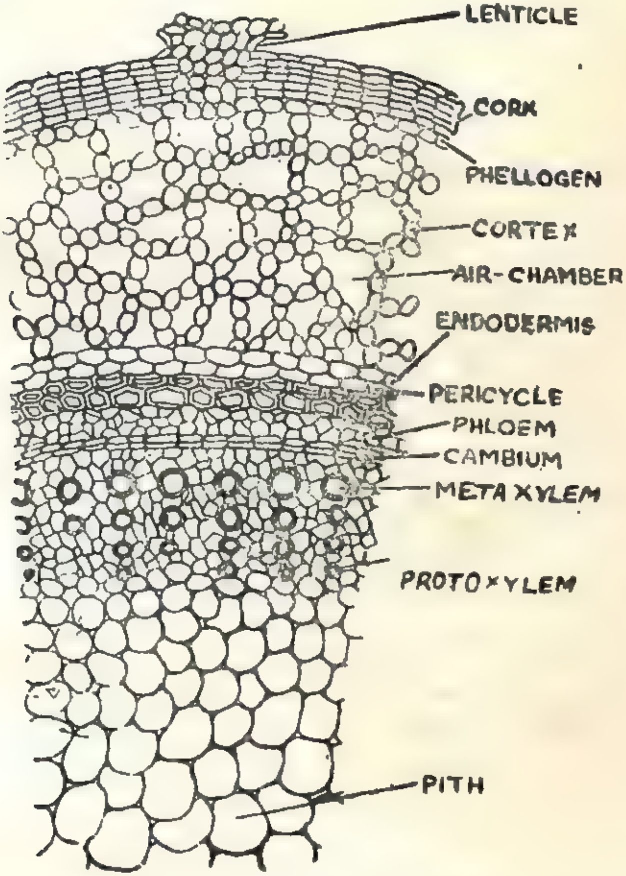


Fig. 9·6. B—T.S. of a Pneumatophore.

(*vi*) Pneumatophores develop a number of lenticels on their surface. The cortex is spongy and consists of extensively developed aerenchyma enclosing large air chambers. Highly developed air chambers are continuous with the stomata of leaves and with the cortex and primary phloem of the stems. Pneumatophores show variations in their internal structures. Generally they show conjoint, collate-

ral vascular bundles with endarch xylem at maturity. Very young pneumatophores, however, show root features, *i.e*, exarch xylem and radial arrangement of vascular tissues (Fig. 9.6 B). Generally the negatively geotropic breathing roots show features of stem and not of roots.

4. Physiological adaptations in halophytes

Morphology and anatomy of the halophytes clearly show xeromorphic features in them. Now, these plants are growing in an environment where water is available to the plants in abundance then why xeromorphy develops in halophytes ? Previously physiological drought was believed to be the main cause of development of xeromorphy in halophytes but recent physiological experiments on these plants have proved that xeromorphism in these plants is, apparently, an example of purposeless adaptation. Physiological experiments make it clear that the halophytes do not experience difficulties, whatsoever, in absorbing too saline water. This point is concluded taking into consideration the following reasonable facts :

(*i*) they show high rates of transpiration,
(*ii*) they show exudation of sap that contains dissolved salts,
(*iii*) they develop many shallow absorbing roots.

Saline conditions are not essentially "dry" for all plant species. Under saline conditions sometimes higher transpiration rates have been observed in halophytes than in neighbouring salt hating plants (Delf, 1911 ; Braun Blanquet, 1931).

It should, therefore, be admitted that the halophytes show xeromorphism for enduring high salinity of soil water and also for absorbing waters with perfect ease. The significance of succulence is not so clearly understood. Probably it is induced by accumulation of salts in cytoplasm. It seems reasonable because of the fact that sodium salts if present in the soil water will definitely stimulate succulence even in non-halophytes and characteristic succulence of some plants may disappear if they are grown on the soil lacking in common salts. Excessive accumulation of sodium does not harm these plants. Halophytes grow in saline habitats not because they are salt loving, but because they tolerate high concentration of salt better than other plants of non-saline habitat. Active accumulation of salts also increases the osmotic concentration of cell sap in these plants and thus makes them able to absorb salty water very easily.

Succession of mangrove vegetation in sea coast

The distribution of a halophytic community appears to be

limited by salinity and depth of water table, as well as by competitive ability of the members of next community in the halosere (Reed, 1947). The aggressiveness of plant communities in saline habitat is due to changes in the salinity level.

In coastal region, nature of vegetation is greatly affected by the gradual elevation of sea coast. Succession of mangrove formation in coast regions may take place very slowly in the following sequence :

(1) In the deep water generally true mangroves, *e. g.* the species of *Avicennia* grow.

(2) When the bottom of the sea is slightly raised up, *Avicennia*, *Rhizophora*, *Ceriops*, *Bruguiera*, etc. form mixed mangroves vegetation in the shallow water.

(3) As the ground is exposed, true mangroves disappear and other halophytes, *e. g.*, species of *Aegiceras*, *Excoecaria* etc. gradually invade the land within short period. These halophytic communities are interspersed by salt tolerating succulents and the grasses make the soil fit for the cultivation of some crop plants. Several varieties of paddy, such as *Oryza sativa var*, *achra*, wild species of *Oryza coarctata* grow very well in these areas.

Succession of angiospermic halophytes varies also in each habitat in accordance with other ecological conditions besides salinity. Thus in reality, there is no general trend for development of various halophytic plant communities around the world and local variations are encountered in each specific site (Yoav Waisel, 1972).

QUESTIONS

1. What are halophytes ? Describe the various characteristic features of halophytes. How do they resemble xerophytes and hydrophytes ?

2. Write short notes on :

Mangrove, vivipary, Pneumatophore, Physiological adaptation of halophites.

3. Discuss briefly the classification of halophytes and give an account of distribution of mangrove vegetation in India.

4. What are the various anatomical features which characterise halophytes ?

5. How is it that mangrove plants show xerophytic structures in spite of abundance of moisture in the habitat ?

10

PRINCIPLES OF PHYTOGEOGRAPHY CLIMATE, VEGETATION AND BOTANICAL ZONES OF INDIA

Principles of phytogeography

Phytogeography or Plantgeography is a science wich deals with the distribution of plants on or near the surface of the earth and water. On the basis of area of the earth surface occupied by the plants, the various taxa are categorised as under :

1. Wides.
2. Endemics.
3. Discontinuous species.

1. **Wides**. Plants widely distributed over the earth in definite climate zones and in different continents are referred to as wides. Cosmopolitan is applied for wides but in fact no plant is truly cosmopolitan in real sense of the term. *Taraxacum officinale* and *Chaenopodium album* are the common examples of the wides. Plants of tropical regions are called *Pantropical*. The plants of very cold climate may not only be found in the arctic regions but also in alpine zone of mountains in tropical and subtropical regions. These are called *arctic-alpine* plants.

2. **Endemics**. Plant species restricted to definite small regions are referred to as endemics. According to area of distribution the species may be continental endemics (restricted to a continent), endemic to a country, provincial, regional or local endemics (restrict-

ed to valley, hills, islands, etc). The important factors responsible for endemism are as follows :

(*i*) Endemics may be the surviors of once widely distributed of ancestral forms for example, *Ginkgo biloba* (restricted to China and Japan), *Sequoia sempervirens* (confined to coastal valleys of California, U.S.A.). *Agathis australis*, *Metasequoia* (confined to Single valley in China). These species are called *Paleoendemics* or *epibionts*. A great majority of the endemic species belonging to this type have many fossil relatives. Because of little variability the endemics are adapted only to a particular environment and even if they reach to new areas, they fail to establish themselves in new environment.

(*ii*) The other endemics may be modern species which have not had enough time for occupying a large area through migration. They are called *neoendemics*. There are several such genera which are widely endemic or few species of which are endemic. Some of the well known endemic genera in Indian flora are *Mecanopsis* (Papaveraceae), Chloroxylon (Rutaceae), Catenaria and Butea (Papilionaceae), Caesulia (Compositae), Petalidium (Acanthaceae) etc. *Elettaria repens* (Zingiberaceae), Piper longum (Piperaceae), *Piper nigrum* (Piperaceae), *Ficus religiosa* (Moraceae), *Shorea robusta* (Dipterocarpaceae), Vanda caerulea (Orchidaceae), *Salmalia malabarica* (Bombacaceae), *Eleusine coracana* (Gramineae) are the well known endemic species of Indian flora.

Endemism results from the failure on the part of species to disseminate its seeds, fruits, spores or propagules because of existence of great barriers like mountains, oceans and large deserts. The oceanie islands which are isolated from rest of the world by large expanses of water abound in endemic species and water barrier checks the migration of these species outside their original habitat.

3. **Discontinuous species**. There are plants which occur at two or more distant places separated by overlands or oceans, hundreds or thousands of miles. Such distribution is called discontinuous or disjunct. The significant phytogeographical causes for discontinuous distribution are as follows :

(*i*) The species might have evolved at more than one place and they failed to migrate outside their original habitats because of barriers.

(*ii*) The species which were once widely distributed in the past disappeared from certain areas and are new surviving in some distant pockets.

(*iii*) **Continental drifts.** The present continents on the earth are not the same as they were in geological past, as for example, during the mesozoic era South America, Africa, India, Polynesia, Australia and Antarctica were all united to form a large landmass called *Gondwanaland* which was having its characteristic flora and fauna. Similarly, there was a northern landmass called *Laurasia* separated from Gondwana land by Tethys sea. Because of geological disturbances the large landmasses gave rise to widely separated continents all having some common species.

(*iv*) The climate may also be a reason for discontinuity in distribution of species. Plants having specific climatic requirements are found in widely separated areas with similar environmental conditions, as for example, plants of arctic regions are also found in alpine zone of high mountains in tropics and subtropics. *Salix* and *Silen* species show discontinuous distribution in arctic-alpine regions.

Factors affecting distribution of species

Several factors are known to affect the geographical distribution of plant species, some of which are as follows :

1. Geological history and distribution,
2. Migration.
3. Ecological amplitude.

1. **Geological history and distribution**. The place where a species first originated is called its centre of origin. Evolution of species is a slow but continuous process. Some of species in present day flora are quite old while a great majority of them are recent in origin. The process of species differentiation involves (*i*) hybridization between the related species as well as mutation and (*ii*) the natural selection from the hybrid and mutant populations. In the selection process not all the hybrids and mutants are selected by nature and only the fittest individuals which find the habitat conditions within their ecological amplitudes are selected and the individuals least fit are eliminated. Changing climate has also played important role in the origin of new species. In the course of evolution several old species became extinct. Some of which can be found today as fossils. The fossils provide direct evidence for the existence of various taxa.

2. **Migration**. The newly evolved species starts migration in newer areas and side by side it undergoes further evolutionary changes. The dispersal of germules and propagules is brought about by several agencies like wind, water, glaciers, insects,

animals and even man. The dispersal is followed by *ecasis*. Migration may be adversely affected and sometimes even totally stopped by some factors called *migration barriers*. Barriers in the dispersal of species may be classified as ecological or environmental and geographical. The climate, an ecological barrier, plays important role in distribution and establishment of species. Unsuitable climatic condition or change of climate in particular area forces the species to migrate from one place to another and the failure of some species to migration leads them to gradual extinction. Besides climate, there are geographical barriers, as for example, high mountains, vast oceans or deserts. The fresh water plants for example cannot be dispersed across oceans if the propagules are suitable only for fresh water dispersal and similarly germules or propagules of land plant from one country cannot reach to other country separated by vast oceans and mountains. Species are called native in the place of its occurrence if it originated there. Outside the area of its origin, the species is referred to as exotic. Exotic species reach to new area through migration. If any species is introduced intentionally in new area by man then it is called introduced species.

3. **Ecological amplitudes and distribution.** Environmental conditions not only influence the life and development of a plant but also determine the presence or absence, vigour or weakness and relative success or failure of various plants in a particular habitat. Each plant species of a community has a definite range of tolerance towards physical and biological environment (its ecological amplitudes) of the habitat.

The presence of species at a particular place, no doubt, indicates that the environmental conditions of that habitat are within its ecological amplitude but the absence of a species from one place does not necessarily indicate that the environment is not suitable for that species.

The ecological amplitude is governed by genetic set up of the species concerned and thus different species have different ecological amplitudes which may sometimes overlap only in certain respects. Further, some species may occur at different geographical regions as and when the conditions fall within its ecological amplitude. As for example, some plants of temperate region, say conifers, may be found in alpine zone of high mountains in tropical and subtropical regions. The other consideration in ecological amplitude as a factor in plant distribution is its change with time. In sexually reproducing plants the hybridization between related species results in offsprings with new genetic composition. With the change of environment the plant

species also make adjustments with new environment by shifts in their ecological amplitudes facilitated by changes in the genotype. Within a species there may occur several genetically different groups of individuals (populations) which are adjusted to particular set of ecological conditions. These populations are called ecotypes or ecological races or ecological population. In *Euphorbia thymifolia* for example, there are two major population—one is calcium loving or calcicole and the other type is calcium hating or calcifuge. Similarly ecological races of *Xanthium strumarium* and *Ageratum conyzoides* differ in their photoperiodic requirements. The existence of ecotypes within the species widens the area of its geographical distribution.

Climate and Vegetation of India

Atmospheric and meteorological influences principally moisture, temperature, wind, atomspheric pressure and evaporation of a region collectively form the climate. Climate has marked influences on the growth, distribution and development of vegetation types in India. India lies north of equator between latitudes 6° and 38°. The Himalayan mountain is present in the north. India is surrounded on its south, east, and west by Indian ocean, Bay of Bengal and Arabian sea respectively. The country as a whole can be divided into three main parts : (*i*) The mountain wall, (*ii*) The plains of northern India, and (*iii*) the plateau of Peninsular India.

Climate of India is not homogeneous throughout but it is highly variable. The country stands in the tropical and subtropical belts and the climate is greatly modified by oceans and mountain ranges. The climate in South and East is more typically tropical rainy, near temperate at high altitudes in the north (Kashmir) and semiarid and arid (dry hot) in the north-western part. The temperature is usually high throughout the year in most part of the country except at high altitude in extreme north where snowfall occurs during winter and temperature goes below 0°C for short periods.

The amount of rainfall varies greatly in different periods of the year and in different parts of the country ; some parts receiving above 400 cm annual rainfall and some receiving as little as 20 cm annual rainfall or even no rains at all in some years. The distribution of annual rainfall in India is shown in Fig. 10·1.

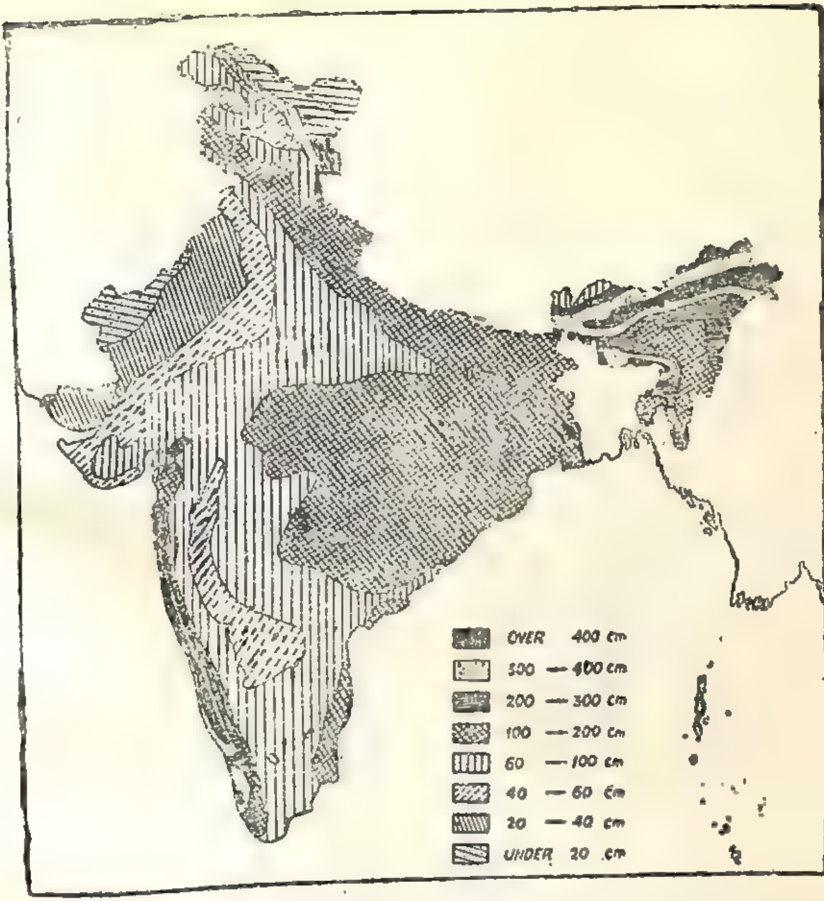


Fig. 10·1. Annual Rainfall

BOTANICAL ZONES OR PHYTOGEOGRAPHIC REGIONS OF INDIA

Vegetation of any place is modified by the environmental factors; climate, geology and biotic factors. The great area of Indian subcontinent has wide range of climate and corresponding diversity in the vegetation. Important contributors who atttempted to analyse the vegetation of India are Hooker (1907) and Chatterjee (1939).

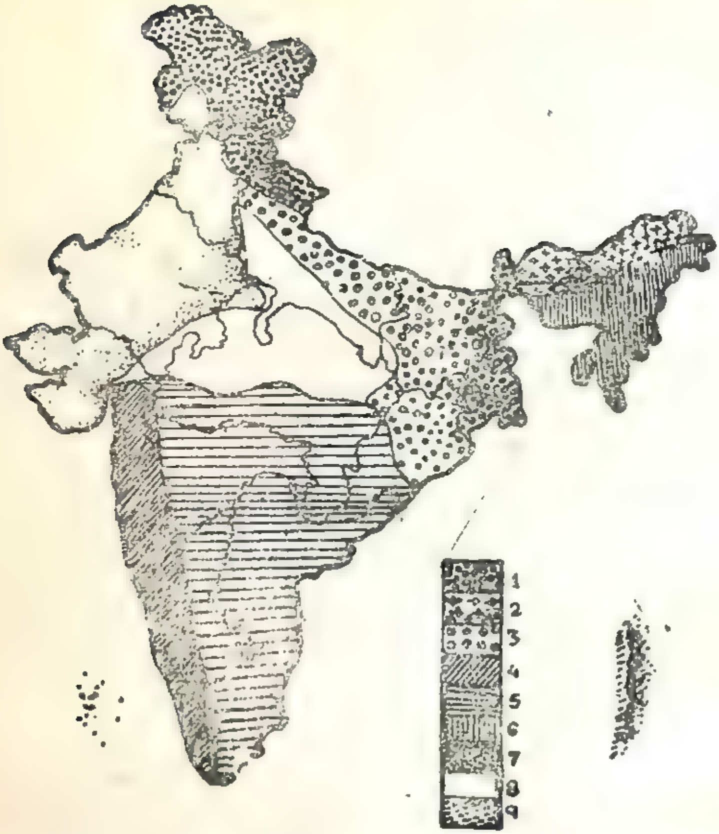


Fig. 10.2 Vegetation of India.

1. Western Himalayas, 2. Eastern Himalayas, 3 Gangetic plain, 4. Western Coast of Malabar, 5. Deccan, 6. Assam, 7. Indus plain, 8. Central India, 9. Bay Islands of Andaman and Nicobar.

Recently India (after partition) has been divided into the following botanical provinces by D. Chatterjee (1962), Fig. 10.2.

(1) Western Himalayas
(2) Eastern Himalayas
(3) Indus plain
(4) Gangetic plain
(5) Central India
(6) Deccan
(7) Western coast of Malabar
(8) Assam
(9) Bay Islands of Andaman and Nicobar (India).

(1) Western Himalayas

The northern part of our country is bounded by highest ranges of Himalayas which is one of the important botanical regions of the world with climate and vegetation ranging from truly tropical near the low altitudes to temperate arctic types at the high altitudes. The northern mountain division can phytogeographically be divided into western, central and eastern zones.

Western Himalayas consist of north Kashmir, south Kashmir, a part of Punjab and Kumaon. This zone is wet in outer southern ranges and slightly dry in inner northern zone. The average annual rainfall in this region is from 100 to 200 cm. Snowfall occurs in this region during winter season. The region may be divided into three subzones (Fig. 10.3 on page 130).

(*i*) *Submontane zone* or *lower region* or tropical and subtropical belts (upto about 1500 metres altitudes from the sea level).

(*ii*) *Temperate zone* (from 1500 metres to 3500 metres altitudes).

(*iii*) *Alpine zone* (above 3500 metres and upto the line of perpetual snow).

(i) Submontane or Lower region or tropical and subtropical belts. It includes outer Himalayas particularly region of Siwaliks and adjoining areas where annual average rainfall is over 100 mm. This zone ranges between 300 metres and 1500 metres. In this zone forests dominated by timber trees of *Shorea robusta* are common. Other important tree species are *Salmalia malabaricum*, *Butea monosperma*, *Acacia catachu* and *Zizyphus* species. In the swampy areas, *Dalbergia sisso* (Shisham), *Ficus glomerata*, *Eugenia jambolana* are common in occurrence. In west dry regions, sal trees are replaced by xeric plants particularly *Zizyphus*, *Carissa*, *Acacia*, and thorny *Euphorbias*. At higher elevation, around 1000 to 1500 metre altitude, cheer (pine) forests are also found at certain places. The common species of pine are *Pinus longifolia* and *Pinus roxburghii*. Ground vegetation is scanty.

(ii) Temperate zone. It commonly ranges at the altitudes from 1500 to 3500 metres above the sea level. Oaks are dominant along with *Populus*, *Rhododendron*, *Betula*, *Pyrus Pinus excelsa*, *Cedrus deodara*, *Picea*, *Abies*, *Cupressus*, and *Taxus baccata* are found in the heavy rainfall region (between 1600 and 1800 m). Herbs are also common in this region. Common herbs are *Ranunculus hirtila*, *Polygonum*, *Pedicularia*, *Potentilla argyrophylla*, *Delphinium*, *Clematis*, crucifers and many members of compositae. In cultivated drylands

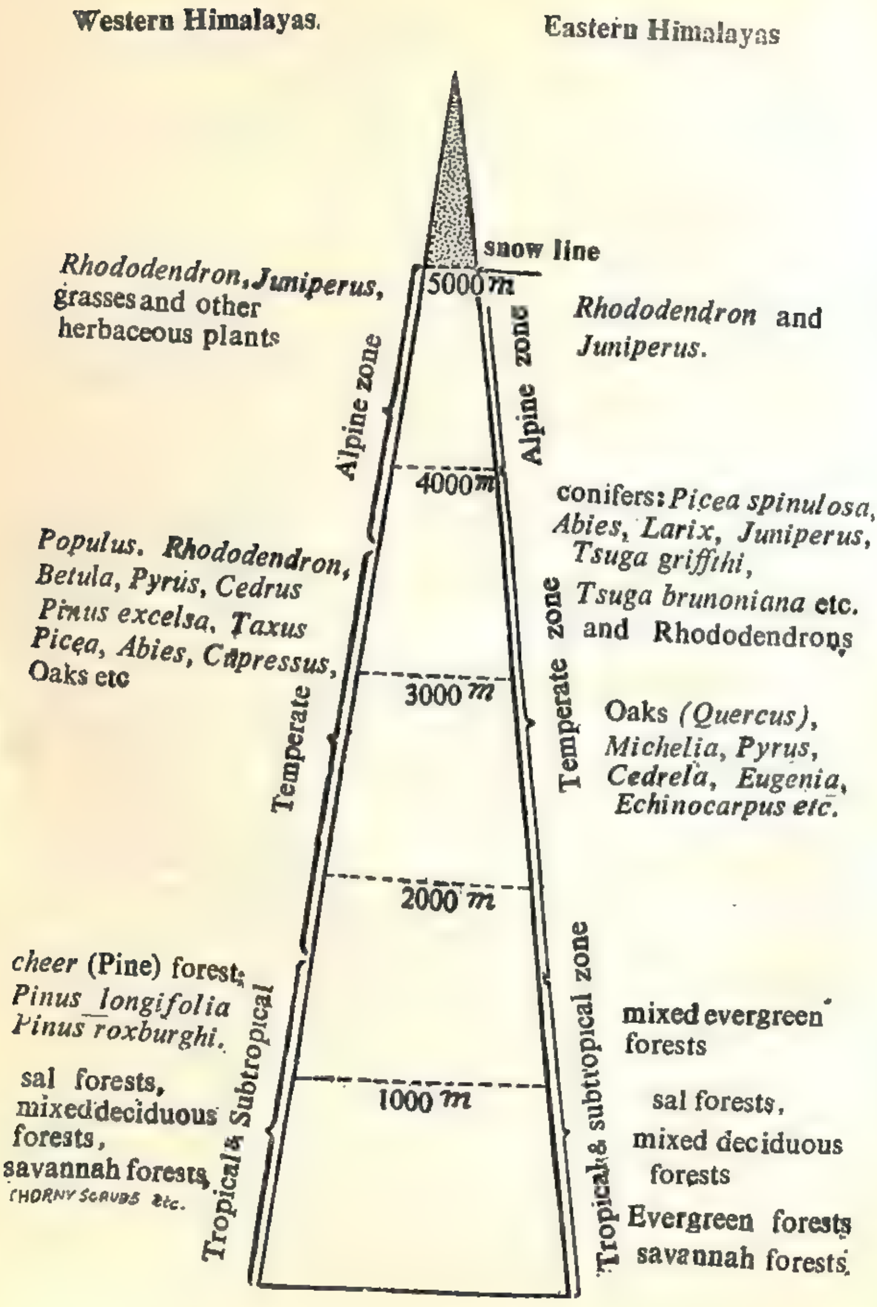


Fig. 10.3—Main types of vegetation at different altitudes in the Western and Eastern Himalayas.

of Punjab, wheat and barley are main crops. In Kashmir, *Bitula* (Birch), Salix (cane), *Populus* (Poplar) are of common occurrence. Besides these, *Quercus semicarpifolia, Q. dilatata, Aesculus indica* (chestnut), and many conifers are commonly met with in this region. In west Kashmir, rice cultivation is common, Keshar or saffron (*Crocus-sativus*), apples, peaches, walnut, almonds and other fruits are important economic plants of Kashmir region.

(iii) Alpine zone. Above the altitude of 3500 metres and up to snowline (about 5000 m) is alpine zone. The vegetation consists of evergreen conifers and some low and broad leaved trees. The vegetation of this region is characterized by cushion habit, dwarf nature and gregarious habit. In lower alpine region, shrubby forests are common which may be (*a*) Birch—fir forest which is fairly dense and is mixed with evergreen shrubby *Rhododendron* at higher level and (*b*) Birch—*Rhododendron* forests in which *silver fir*, *Betula*, *Rhododendron* and *Junipers* are common. In the upper alpine region, prominent herbaceous plants are the species of *Primulas*, *Polygonum*, *Gentiana*, *Cassiope*, *Meconopsis*, *Saxifraga*, *Potentilla*, *Geranium*, *Aster*, *Astragalus* etc. which form alpine meadows. At about 5000 metre altitude and above, snow perpetuates round the year and plant growth is almost nil. This altitude is called snow line or iceline.

Populations of *Draba*, *Braya*, *Cortia*, *Leontopodium* go on increasing with the increase in altitude. Species of *Ephedra*, *Juniperus*, *Barberis* are also found scattered. *Poa*, *Stipa* and *Pectuca* are common grasses of alpine zone.

(2) Eastern Himalayas

Eastern Himalayas extend from Sikkim to upper Assam, Darjeeling and NEFA. Vegetation of this region differs from that of western Himalayas. The chief differences are due to changed environmental factors as heavy monsoon rainfall, less snowfall and high temperature and humidity. This region can also be divided into (*i*) Tropical submontane zone (*ii*) Temperate or montane zone, and (*ii*) Alpine zone (Fig. 10.3.)

(i) Tropical or Submontane Zone. This tropical subzone characterized by warm and humid conditions extends from plain up to the altitude of about 1800m. In this zone mostly sal forests, mixed deciduous forests consisting of important plants, such as *Sterculia*, *Terminalia*, *Anthocephalus cadamba* and *Bauhinia* are common. In the savannah forests, common plants are *Albezzia procera*,

Bischofia, Salmelia, Dendrocalamus. Evergreen forests of *Dillenia indica, Michelia champaca, Echinocarpus, Cinnamon* etc. are common.

(ii) **Temperate or Montane Zone.** It may be further divided into upper and lower zones. Lower temperate zone is the region between 1800 and 3000 metre altitudes. In the lower temperate zone, Oaks (*Quercus*), *Michelia, Pyrus, Cedrela. Eugenia, Echioncarpus* are common plants. In upper temperate zone (300-400 metre altitude), conifers and rhododendron are common. Important conifers of this region are *Picea spinulosa, Abies, Larix, Juniperus, Tsuga griffithi, Tsuga brunoniana, etc.*

(iil) **Alpine Zone (from 4000 metres up to snow line).** Climate is humid and extremely cold. The vegetation in the alpine zone is characterised by complete absence of trees and predominance of shrubs and meadows. Important plants of this zone are *Rhododendron* and *Juniperus.*

Eastern Himalayan vegetation is considered to be one of the richest vegetational units in the world and consists of several species of plants which are native of foreign countries, such as, China, Japan, Burma, Malaya and European countries.

(3) Indus Plains

It includes part of Punjab, Rajasthan, Cutch, Delhi, a part of Gujarat. Some part of this plain is now in west Pakistan. The climate of this zone is characterised by dry hot summer, and dry cold winter. Rainfall is usually less than 70 cm, but in certain regions it is as low as 10-15 cm. The soil of a wide area except cultivated land is saline. Much of the land has become desert due to excessive dryness.

Vegetation is mainly bushy and thorny. *Acacia arabica, Prosopis spicigera, Salvadora, Capparis decidua* are very common plants of this region. *Salsola phoetida* and *Lunakh grass* are found mostly in saline soils. Other plants of this botanic province are *Anageissus, Eugenia*, Mango, *Dalbergia sisoo, Albizzia lebbek, Zizyphus, Numularia etc.*

Historical evidences indicate that the area was covered by dense forest some 2000 years ago, but gradual destruction of vegetation cover either by biotic agencies or by any other agency led to the development of desert in this plain. *Saccharum munja, Cenchrus ciliaris, Prosopis spicigera, Acacia leucophloer A. senegal* are the important plant species which are grown for checking the spread of desert.

(4) Gangetic Plains

This is one of the richest vegetational zones in India. This zone covers flat land of a part of Delhi, whole of U. P., Bihar, West Bengal and also a part of Orissa. Rainfall in this zone is from 50 cm to 150 cm.

A great part of the land is under cultivation. The common crop plants are wheat, barley, maize, *Sorghum* (jowar), bajra, urad, moong (*Phaseolus mungo*), *Cajanus cajan*, til (*Sesamum indicum*), sugarcane, pea (*Pisum sp.*), gram (*Cicer arietinum*), potato, *Brassica*, rice.

In western part of U. P., annual rainfall is from 50 cm to 110 cm. Dry deciduous and shrubby forests are common in this part. Important plants of south-western part of U. P. are *Capparis. Saccharum munja, Acacia arabica*. In the north-western part of U. P. near Himalayan foothills, *Dalbergia sisoo, Acacia arabica* are most common plants.

In eastern gangetic plain, the conditions are cold and wet (rainfall, 150 cm in West Bengal). In this part, evergreen forests are common. In central part, the annual rainfall is about 100 to 150 cm. The vegetation consists mainly of deciduous trees. Sal trees are dominant. Other common trees are *Terminalia tomentosa, T. belerica, Acacia* species, *Bauhinia, Diospiros* (Biri ka patta or tendu), *Eugenia* sp., neem trees (margosa), *Madhuca indica* (Mahua), *Cordia myxa* (Lasora), *Tamarindus, Mango* (*Mangifera indica*), *Ficus etc.*

In Bihar and Orissa hills—*Rubus—Potentialla, Fragaria* (*Rosaceae*), *Pyrus* etc. are also common. Mangrove vegetation is common in tidal region in West Bengal near Sunderbun, *Rhizophora mucronata, R. Conjugata, Sonneratia, Ceriops roxburghiana*, and *Acanthus ilicifolius, Kandelia rheedii, Bruguiera gymnorhiza* are common mangrove plants in this zone.

(5) Central India

Central India covers Madhya Pradesh, part of Orissa, Gujarat and Vindhya. The areas are hilly. The average rainfall per annum may be 100-170 cm. Some places are at the altitudes of 500-700 m from the sea level. Biotic disturbances are very common in this botanical province which have led to the development of the thorny vegetation in open areas. In this region, teak (*Tectona grandis*) is very common. Other trees are (*Terminalia tomentosa, Bauhinia,*

mango, *Phyllanthus*, *Ficus glomerata etc*. Among common shrubs are *Mimosa rubicaulis*, *Desmodium*, *Acacia sp*., *Zizyphus rotundifolia* and others. Entire forest vegetation of central India may be divided into (*i*) sal forest, (*ii*) mixed deciduous forest, and (*iii*) thorny forest.

At Sarguja (M. P.) many species have been reported to occur. Some of them are *Pyrus*,*Barberis asiatica*, *Rubus elipticus etc*.

(6) Deccan

This region comprises whole of the southern peninsular India including Satpura and southern part of Godawari river. Average annual rainfall in this region is about 100 cm. It may be divided into the following two subdivisions :—

(*i*) Deccan plateau
(*ii*) Coromandel coast.

In Deccan plateau, teak forests containing *Diospiros*, *Acacia*, *Prosopis spicigera*, *Santalum* (chandan tree) and *Cedrela toona* are common. On rocks, *Capparis*, Euphorbias, *Phyllanthus* are common. Teak, *Pterocarpus*, *Borassus*, *Foenix silvestris* are also common in this area. In Chota Nagpur plateau, important species are *Clematis natans*, *Barberis*, *Thallictrum* and also many members of Annonaceae Rosaceae, Compositae, Araliaceae, Apocynaceae, Lauraceae, Amaranthaceae Orchidaceae. Some ferns are also common.

In Coromandel coast vegetation consists largely of some halophytic species.

(7) Western coast of Malabar

This is a small botanical province covering Cape Comorin to Gujarat and Western Ghat. This is a region of heavy rainfall. In this zone, four types of forests are common :

(*i*) *Tropical forests* (occur at 700 m altitude),
(*ii*) *Mixed deciduous forests* (found at the altitude up to 1600 m),
(*iii*) *Temperate evergreen forests* (occur at most than 1200 m altitude), and
(*iv*) *Mangrove vegetation*.

In tropical evergreen forests the trees are tall and they have root buttresses. Important species are *Cedrela toona*, *Dipterocarpus*, *Magnifera indica*, *Sterculia alata*, *Artocarpus hirsuta*. In the mixed

deciduous forest, important plants are *Terminalia tomentosa, Terminalia peniculata, Tectona grandis, Dalbergia, Lagerstroemia lanceolata* and bamboo species particularly *Dendrocalamus* and *Bamboosa arundinacea*. On the Nilgiri hills subtropic and temperate conditions exist. Important plants of Nilgiri vegetation are *Rubus, Rhododendron arboreum, Barberis, Thallictrum, Ranunculus, Fragaria, Potentilla*. Many other herbs alongwith many grasses are also common

Temperate forests commonly called as "Sholas" contain *Gardenia obtusa, Michelia nilgirica. Eugenia* species are also common. In Malabar, plants belonging to family Dipterocarpaceae, Teliaceae, Anacardiaceae, Meliaceae, Myrtaceae, Piperaceae, Orchidaceae and many ferns are common. The west coast of Malabar region receives very high rainfall. In the coastal region mangrove plants grow luxuriantly.

(8) Assam

This botanical province is very rich in vegetation and covers valley of Brahmputra, Naga hills and Manipur. This is the region of heaviest rainfall. Cherapunji is one of the rainiest places of the world—rainfall often exceeds 1000 cm. Excessive wetness and high temperature in the zone are responsible for the development of dense forests. Broad leaved tall evergreen angiosperms and some conifers are very common in the forests. Common plants occurring in this region are *Ficus, Artocarpus, Michelia champaca, Sterculia alata, Morus* species. Besides these, Bamboos, canes, climbers, and green bushes are also common. Prominent plants in the northern forest of this zone are *Alnus nepalensis, Betula, Rhododendron arbəreum. Magnolia, Michelia* and *Prunus*. Sal also occurs at Garo hills. Orchids and fern species are very rich in this zone.

(9) Bay Islands of Andaman and Nicobar (India)

These bay islands represent elevated portions of submarine mountains. Climate is humid in the coastal region. In Andaman, beech forests, evergreen forests, semi-evergreen forests, deciduous forests and mangrove vegetation are of common occurrence. *Rhizophora, Mimusops, Calophyllum*, etc., are common plants in mangrove vegetation. In the interior, evergreen forests of tall trees are common. Important species of trees are *Calophyllum, Dipterocarpus, Lagerstroemia* and *Terminalia, etc.* Some part is under cultivation. The important crops are paddy and sugarcane.

QUESTIONS

1. What are phytogeographical principles ? Discuss in brief the factors which affect distribution of plant species.
2. Write short notes on :
   (*a*) Discontinuous distribution on species.
   (*b*) Endemism.
3. Describe tho climate of India and their bearing in distribution of plant formations .
4. Describe the various forest communities of India.
5. Give an account of grassland vegetation in India.
6. Describe in brief different phytogeographic regions of India.
7. Describe the vegetation of Eastern or Western Himalayas.